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BAND 69

NEW GENERIC NAMES PROPOSED IN THIS VOLUME

	Page
Ianiroides Kensley, 1976	295
Ianisera Kensley, 1976	297
Inguza Simpson, 1975	71

LIST OF CONTENTS

Page

Barghusen, H. R.
Notes on the adductor jaw musculature of *Venjukovia*, a primitive anomodont therapsid from the Permian of the U.S.S.R. (Published June 1976.) 249

Bouillon, J. *see* Millard, N. A. H.

Cluver, M. A. *see* Galton, P. M.

Galton, P. M. & Cluver, M. A.
Anchisaurus capensis (Broom) and a revision of the Anchisauridae (Reptilia, Saurischia). (Published April 1976.) 121

Harris, J. M.
Pliocene Giraffoidea (Mammalia, Artiodactyla) from the Cape Province. (Published September 1976.) 325

Hendey, Q. B.
The Pliocene fossil occurrences in 'E' Quarry, Langebaanweg, South Africa. (Published April 1976.) 215

Kennedy, W. J. *see* Klinger, H. C.

Kensley, B.
Records of mud-prawns (genus *Callianassa*) from South Africa and Mauritius (Crustacea, Decapoda, Thalassinidea). (Published December 1975.) 47

Kensley, B.
Isopodan and tanaidacean Crustacea from the St Paul and Amsterdam Islands, southern Indian Ocean. (Published June 1976.) 261

Klinger, H. C., Kennedy, W. J. & Siesser, W. G.
Yabeiceras (Coniacian ammonite) from the Alphard Group off the southern Cape coast. (Published March 1976.) 161

Millard, N. A. H. & Bouillon, J.
Additional hydroids from the Seychelles. (Published December 1975.) 1

Siesser, W. G. *see* Klinger, H. C.

Simpson, G. G.
Notes on variation in penguins and on fossil penguins from the Pliocene of Langebaanweg, Cape Province, South Africa. (Published December 1975.) .. 59

Tankard, A. J.
Thermally anomalous Late Pleistocene molluscs from the south-western Cape Province, South Africa. (Published August 1975.) 17

Tankard, A. J.
Pleistocene history and coastal morphology of the Ysterfontein–Elands Bay area, Cape Province. (Published March 1976.) 73

Van den Heever, J. A.
The cranial and cervical muscles of the South African limbless lizard *Typhlosaurus aurantiacus aurantiacus* Peters (Reptilia, Sauria). (Published April 1976.) .. 169

VOLUME 69 PART 1 DECEMBER 1975 ISSN 0303-2515

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THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* **4**: 269–270. Jena: Fischer.—*Denkschr. med.-naturw. Ges. Jena* **16**: 269–270.

(continued inside back cover)

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ADDITIONAL HYDROIDS FROM THE SEYCHELLES

by

N. A. H. MILLARD

&

J. BOUILLON

Cape Town Kaapstad

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ADDITIONAL HYDROIDS FROM THE SEYCHELLES

By

N. A. H. Millard
South African Museum, Cape Town

&

J. Bouillon
Universite Libre de Bruxelles

(With 3 figures)

[*MS. accepted 16 April 1975*]

ABSTRACT

This paper supplements an earlier one on the hydroids of the Seychelles and records ten more species. In addition three new species are described, namely *Egmundella modesta*, *Hebella muscensis* and *Scandia tubitheca*. The last two have identical trophosomes but different gonosomes, and arising from this it becomes necessary to consider *Campanularia costata* Bale, 1884 and *Campanularia corrugata* Thornely, 1904 as *nomina oblita* since these were both described on sterile material.

CONTENTS

	PAGE
Introduction	1
List of species	2
Systematic section	3
Acknowledgements	14
References	14

INTRODUCTION

The hydroids described in this paper were collected by the second author during an expedition to the Seychelles Archipelago from June to September 1972. This expedition was financed by the Belgian 'Fonds National de la Recherche Scientifique', the Belgian Ministry of Education and Culture, the 'Musée Royal de l'Afrique Centrale' (Tervuren, Belgium) and the University of Brussels. The collection is the property of the 'Musée Royal de l'Afrique Centrale', where the types of new species have been deposited.

During a previous mission, in 1966, a large quantity of marine invertebrates was collected and from the interest their study aroused we were led to consider another expedition in order to complete our observations and extend them to some islands of the archipelago never before prospected or scarcely so.

As for the hydroids, one paper has already been published by Millard & Bouillon (1973) and another by Bouillon (1974). The present account expands our knowledge of the hydroid fauna of this area.

Ann. S. Afr. Mus. **69** (1), 1975: 1–15, 3 figs.

LIST OF SPECIES

Additional to those described by Millard & Bouillon (1973), together with localities. Those species marked with an asterisk will be discussed further in the pages which follow.

Family **Asyncorynidae**

Asyncoryne ryniensis Warren

A small fertile colony growing inside a dead *Pecten* shell, and bearing several young medusae with cnidophores. Dredged between Silhouette and Mahé.

Family **Cladocorynidae**

Cladocoryne floccosa Rotch

A large number (over 60) of infertile polyps from Praslin growing on sponges.

Family **Pandeidae**

**Amphinema ?rugosum* (Mayer)

A small fertile colony from Anse la Mouche.

Family **Campanulinidae**

**Egmundella modesta* sp. nov.

Family **Haleciidae**

**Campalecium cirratum* (Haeckel)

Three rich and fertile colonies from Anse la Mouche and Praslin.

Family **Lafoeidae**

**Hebella muscensis* sp. nov.
**Scandia tubitheca* sp. nov.

Family **Syntheciidae**

**Hincksella corrugata* Millard

An infertile colony from Bird Island.

**Hincksella cylindrica pusilla* Ritchie

Several stems reaching a maximum height of 8,7 mm from Bird Island.

Family **Sertulariidae**

**Dynamena obliqua* Lamouroux

An infertile colony from Bird Island.

**Sertularella diaphana* (Allman)

A fragment of an infertile stem 1,1 cm in length from Praslin.

Sertularia distans (Lamouroux)

An infertile colony from Bird Island.

Family **Plumulariidae**

Pycnotheca mirabilis (Allman)

Two infertile stems from Bird Island.

In addition new information is provided for the following species:

Family **Bougainvilliidae**

**Silhouetta uvacarpa* Millard & Bouillon

A fertile colony dredged between Silhouette Island and Beau Vallon on Mahé Island, from which newly released medusae were obtained.

Family **Campanulinidae**

**Phialella quadrata* (Forbes)

A fertile colony from Anse la Mouche growing on the stem of *Halocordyle disticha*.

Family **Syntheciidae**

**Synthecium patulum* (Busk)

Three fertile colonies, one dredged between Silhouette Island and Beau Vallon on Mahé Island, and two from Anse la Mouche.

SYSTEMATIC SECTION

Family **Bougainvilliidae**

Silhouetta uvacarpa Millard & Bouillon, 1973

Silhouetta uvacarpa Millard & Bouillon, 1973: 25, fig. 3A–D, pls 2–3.

Description

Newly released medusae reaching a maximum size of approximately 0,9 (depth) × 1,0 mm (diameter) possess four oral tentacles with one dichotomy, and four marginal tentacles. The branching oral tentacles confirm the inclusion of this species in the Bougainvilliidae.

Family **Pandeidae**

Amphinema ?rugosum (Mayer, 1900)

Fig. 1A–D

Amphinema rugosum: Rees & Russell, 1937: 67, figs 5–6. Russell, 1953: 183, fig. 90, pl. 10 (fig. 3), pl. 11 (figs 2, 4). Kramp, 1965: 29.

Description

Solitary hydranths and medusa-buds arising separately from a creeping hydrorhiza. Hydrorhiza with firm perisarc, about 0,03 mm in diameter.

Hydranths up to 3 mm in height, with one row of 10–12 filiform tentacles, contained within a firm perisarcal tube for most of length. Perisarcal tube slender and annulated at base, smooth for the rest and widening distally.

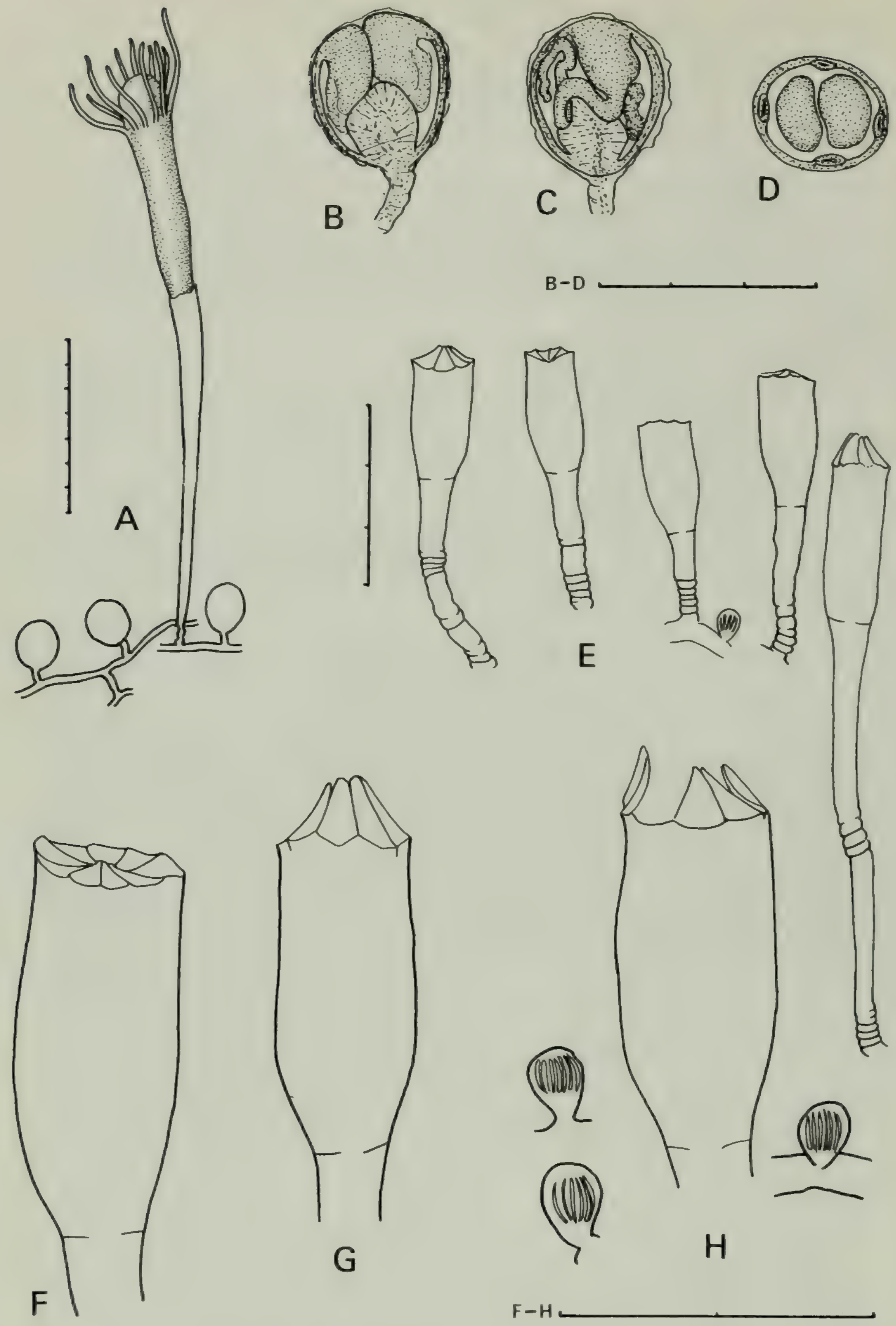

Fig. 1. *Amphinema ?rugosum*. A. Part of a colony sketched from a combination of several damaged hydranths. B–D. Views of medusa-buds from whole mounts, right one viewed from above, showing two tentacles, hypostome and radial canals.

Egmundella modesta sp. nov. E–H. Views of hydranthophores and nematothecae.

Scale in mm/10.

Medusa-buds on short pedicels contained in wrinkled perisarc, oval, with four radial canals and two opposite marginal bulbs bearing coiled tentacles. No oral tentacles.

Measurements (mm)

Perisarcal tube, height	1,41–2,53
diameter at base	0,02–0,04
diameter at distal end	0,09–0,13
Medusa-bud, height .. .. reaching	0,23
diameter .. .. reaching	0,20

Remarks

The medusa-buds, with their two stout marginal bulbs, resemble the genus *Amphinema*, in which the hydranths of *A. dinema* and *A. rugosum* are known (Rees & Russell 1937). Of the two this material is closer to *A. rugosum*, which has stronger perisarc annulated at the base. Both species of medusa occur in the plankton; *A. dinema* is rare and *A. rugosum* very abundant.

Family **Campanulinidae**

Egmundella modesta sp. nov.

Fig. 1E–H

Lovenella sp.: Millard & Bouillon, 1973: 42, fig. 5E–F.

Holotype: an infertile stolonial colony from Anse la Mouche.

Description

Hydrothecae borne singly on the summit of pedicels of variable length. Pedicel increasing in diameter from base to distal end; with thicker perisarc at the base and thinner distally; annulated irregularly, with 2–7 distinct annulations at base and above this smooth or with faintly corrugated areas or with groups of annulations, distal end always smooth.

Hydrotheca deep-campanulate, rounded at base, narrowed above this and widening again at margin. A definite diaphragm present. Operculum of about eight triangular segments clearly demarcated from thecal wall.

Nematothecae scattered on hydrorhiza, one-chambered, obovate to globular, sessile, containing a cluster of large nematocysts.

Hydranth with 15–18 tentacles in the few extended individuals present, with no intertentacular web.

Measurements (mm)

Pedicel, length	0,14–0,71
diameter at base	0,03–0,05
Hydrotheca, depth	0,20–0,33
diameter at margin	0,08–0,11
Nematotheca, depth	0,04–0,05
maximum diameter..	0,02–0,04

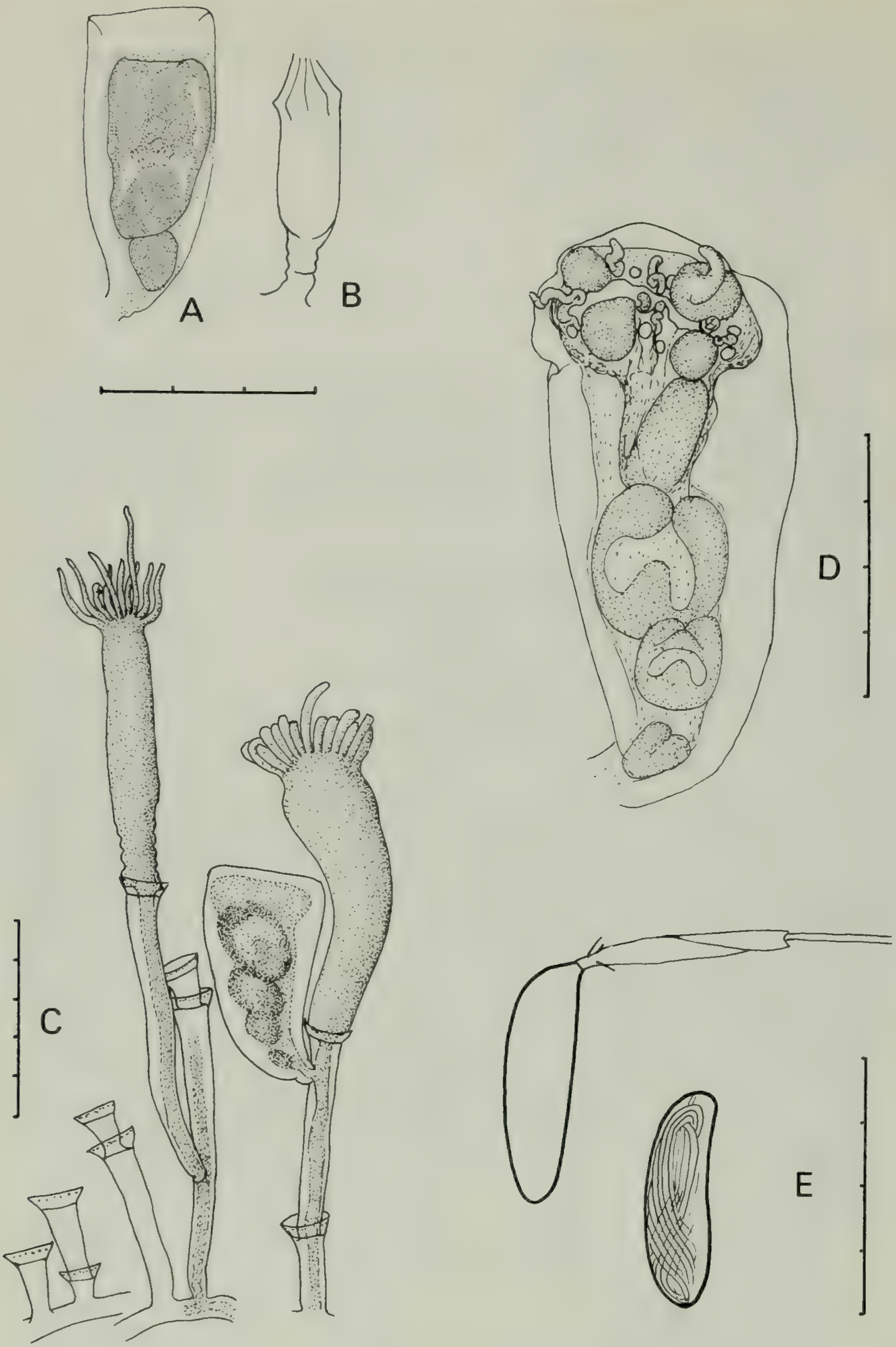

Fig. 2. *Phialella quadrata*. A. Gonotheca containing medusa-buds. B. Hydrotheca. *Campalecium cirratum*. C. Hydranthophores with hydranths and gonotheca. D. Gonotheca with medusa-bud ready to escape. E. Microbasic mastigophore, discharged and undischarged. Scale: A–D in mm/10, E in mm/100.

Remarks

This species differs from *E. amirantensis* in the presence of a well-developed and annulated thecal pedicel and in the sessile nematothecae.

The material is similar to that described by Millard & Bouillon (1973) as ?*Lovenella* sp. Re-examination of this earlier material has established the presence of nematophores in the samples from Praslin although in the original preparation it was not possible to relate them with certainty to the same hydrorhiza.

The structure of the hydrotheca with its diaphragm and well-demarcated opercular segments distinguishes *E. modesta* from other species of *Egmundella*. Indeed the hydrotheca is similar to that of *Lovenella* and the only character definitely distinguishing the hydranth generations of these two genera is the presence of nematothecae in the former.

Phialella quadrata (Forbes, 1848)

Fig. 2A–B

Hypsorophus quadratus: Huvé, 1952: 38, figs 3–7.
?*Phialella quadrata:* Millard & Bouillon, 1973: 43, fig. 5G–J.

Description

Colony stolonial. Hydrothecae similar to those described from Mahé in 1973 and measurements within range.

Gonothecae present, elongated and truncated distally, reaching 0,57 mm in length and 0,24 mm in maximum diameter, containing two medusa-buds, one large and one small. Larger medusa-buds deep, with at least two marginal bulbs and tentacles.

Remarks

The presence of gonothecae, which are exactly like those illustrated by Huvé, supports the identification of this material.

Family **Haleciidae**

Campalecium cirratum (Haeckel, 1879)

Fig. 2C–E

Halecium simplex Pictet, 1893: 22, pl. 1 (figs 16–17). Ritchie, 1910: 807, pl. 77 (figs 10–11).
Campalecium medusiferum Torrey, 1902: 48, pl. 3 (figs 26–29). Huvé, 1954: 183, pls 7–9.
Eucheilota cirrata: Brinckmann, 1959: 82, figs 1–3.
Lovenella cirrata: Kramp, 1961: 177; 1968: 80, fig. 215.
Campalecium simplex: Rees & Thursfield, 1965: 112.

Description

Hydrorhiza reticular or forming long unbranched threads on the surface of sponges and polyzoans, giving rise to hydranthophores at intervals.

Hydranthophores usually solitary and with a single terminal hydranth, occasionally with one or two sympodial branches; often regenerated. Pedicel constricted at base, of very variable length. Hydrotheca with straight walls widening to margin, with a circle of refringent nodules marking attachment of hydranth. Hydranth very large, with 24–30 tentacles and an intertentacular web.

Gonotheca arising from side of pedicel below hydrotheca, curved, widening to truncated distal end, containing three or four medusa-buds one above the other.

Oldest medusa-bud with four perradial marginal bulbs of which two bear tentacles and are slightly larger than the others, and eight adradial statocysts. Although the margin is rather crumpled, in the largest medusa a marginal cirrus is clearly visible next to three of the large marginal bulbs, and four interradial cirri can be identified on rudimentary marginal bulbs.

Large nematocysts (microbasic mastigophores) present in intertentacular web and in gonophores, 33,6 × 7,2 – 36,0 × 9,0 μ. Capsule banana-shaped. Butt with length approximately equal to that of capsule, bearing a raised spiral ridge with small spines on the proximal region. Several other types of nematocyst present in tentacles, but undischarged.

Measurements (mm)

Pedicel, length	0,07–0,99
diameter at base	0,04–0,08
Hydrotheca, depth	0,02
diameter at margin	0,10–0,14
Gonotheca, depth	0,41–0,77
maximum diameter	0,23–0,38

Remarks

Brinckmann (1959) reared medusae of *Lovenella cirrata* (Haeckel, 1879) from the polyp *Haleciella microtheca* Hadži, 1914, which latter Huvé (1954) included as a synonym for *Campalecium medusiferum* Torrey, 1902.

Rees & Thursfield (1965) synonymized *Campalecium medusiferum* with *Halecium simplex* Pictet, 1893 after re-examination of Ritchie's material (1910) of the latter species from Mergui. They used the name *Campalecium simplex*. However, they gave no description of the gonophores and did not comment on Ritchie's statement that the gonangium contained 'ova to the number of about six'. Recently the first author, by the courtesy of the Royal Scottish Museum, Edinburgh, was able to re-examine Ritchie's slides (nos. 1959. 33. 162–171). Although it was not possible to decipher details of structure, the gonothecae clearly contained medusa-buds and not eggs as described and illustrated by Ritchie. We, therefore, confirm Rees & Thursfield's synonymy, but point out that of the available specific names *cirratum* Haeckel, 1879 antedates *simplex* Pictet, 1893, *medusiferum* Torrey, 1902 and *microtheca* Hadži, 1914.

Although the genus name *Lovenella* Hincks, 1868 has precedence over

Campalecium Torrey, 1902, we do not feel that the former can be stretched to contain a Haleciid polyp, and therefore retain the name *Campalecium.* We are here faced with a species in which the polyp generation belongs to one family (Haleciidae) and the medusa to another (Lovenellidae).

The presence of microbasic mastigophores in the species supports the idea of an affinity between the Haleciidae and the Campanulinidae suggested earlier by Millard (1975) and based on the presence of a Lovenellid medusa in *Campalecium* and certain resemblances of hydranth and hydrothecal structure in the two families. These nematocysts, which are by no means common in the Athecata, occur also in *Hydrodendron caciniformis* (personal observation of first author) and *Halecium halecinum* (Weill 1934) among the Haleciidae, and in *Eucheilota maculata* and *Eutonina indicans* among the Campanulinidae (Werner 1968*a*, 1968*b*). Werner suggests that their evolutionary forerunners are basitrichous isorhizas, which are often difficult to distinguish from them and which occur commonly in the Campanulinidae.

The polyp generation of *C. cirratum* is known from the Mediterranean, the Indo-West Pacific (Moluccas, Mergui) and the eastern Pacific (California). This is the first record from the western Indian Ocean. These records, together with those of the medusa from the Mediterranean, various parts of the tropical Atlantic and Malaya (Kramp 1961, 1968), show the species to be circumtropical in distribution.

Family **Lafoeidae**

Remarks on Hebella corrugata and H. costata

Campanularia corrugata Thornely, 1904 was described from a sterile colony from Ceylon. The type material of *Campanularia costata* Bale, 1884 from Port Darwin, with which species Billard (1941) synonymizes *Hebella corrugata*, was also sterile. Since the original description of these two species all material delegated to one or the other has been sterile, except for some empty and probably immature gonothecae described by Billard (1941). In 1973, however, Millard & Bouillon described gonophores in material from the Seychelles, which was attributed to Thornely's species. Since the gonophores were fixed sporosacs and showed no medusoid characters, the species was transferred from *Hebella* to *Scandia*, thus: *Scandia corrugata.*

In this second collection from the Seychelles, material is present with an identical trophosome—it cannot be distinguished from that described in 1973 on measurements or any other character—but with gonothecae containing well-developed medusa-buds. It is apparent, therefore, that there are two species with identical trophosomes and different gonosomes, one a *Hebella* and the other a *Scandia.* Since there is no means of telling to which of these Thornely's and Bale's species belong, the only immediate solution is to create two new species, and to regard *Hebella corrugatum* (Thornely 1904) and *Hebella costata* (Bale 1884) as *nomina oblita.* Sterile material cannot be identified, and all sterile records attributed to either of the two species should be disregarded.

Hebella muscensis * sp. nov.

Fig. 3A–B

Holotype: a fertile colony epizootic on *Synthecium* sp. from Anse la Mouche.

Description

Hydrotheca tubular, curved to one side, with 5–9 transverse annulations, with everted margin usually oblique to axis and lower on the shorter, more concave side. An annular thickening present round base, asymmetrically developed, pronounced on the shorter, more concave side and often not noticeable on the other. Pedicel short, not annulated, but occasionally with an indistinct node separating it from the hydrorhiza.

Gonotheca borne on hydrorhiza on short pedicel, elongated, widening distally, often slightly curved, usually longer than hydrotheca, with transverse annulations which may be somewhat irregular, with an operculum of four segments, containing up to four medusa-buds one above the other. Medusa-bud with rounded hypostome, at least four marginal tentacles and a varying number of ocelli (usually eight).

Measurements (mm)

Pedicel length	0,08–0,17
Hydrotheca, depth, convex side	0,82–1,20
diameter at mouth	0,35–0,53
diameter/depth	0,37–0,50
Gonotheca, length	1,04–1,42
maximum diameter	0,38–0,53

Scandia tubitheca sp. nov.

Scandia corrugata: Millard & Bouillon, 1973: 60, fig. 8D–F (fertile colony only).

Holotype: fertile colony from Amirante, Seychelles, epizootic on *Synthecium dentigerum.*

Diagnosis

Hydrotheca similar to that of *Hebella muscensis.* Gonotheca (only male known) also very similar, but wider distally and not curved, containing a single gonophore in the form of a fixed sporosac.

Family **Syntheciidae**

Hincksella corrugata Millard, 1958

Hincksella corrugata Millard, 1958: 181, fig. 5. Gravier, 1970: 116.

Description

Unbranched stems reaching 8,0 mm and with up to 10 hydrothecae. Structure similar to holotype, but dimensions all slightly less.

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* From Anse la Mouche: Bay of flies.

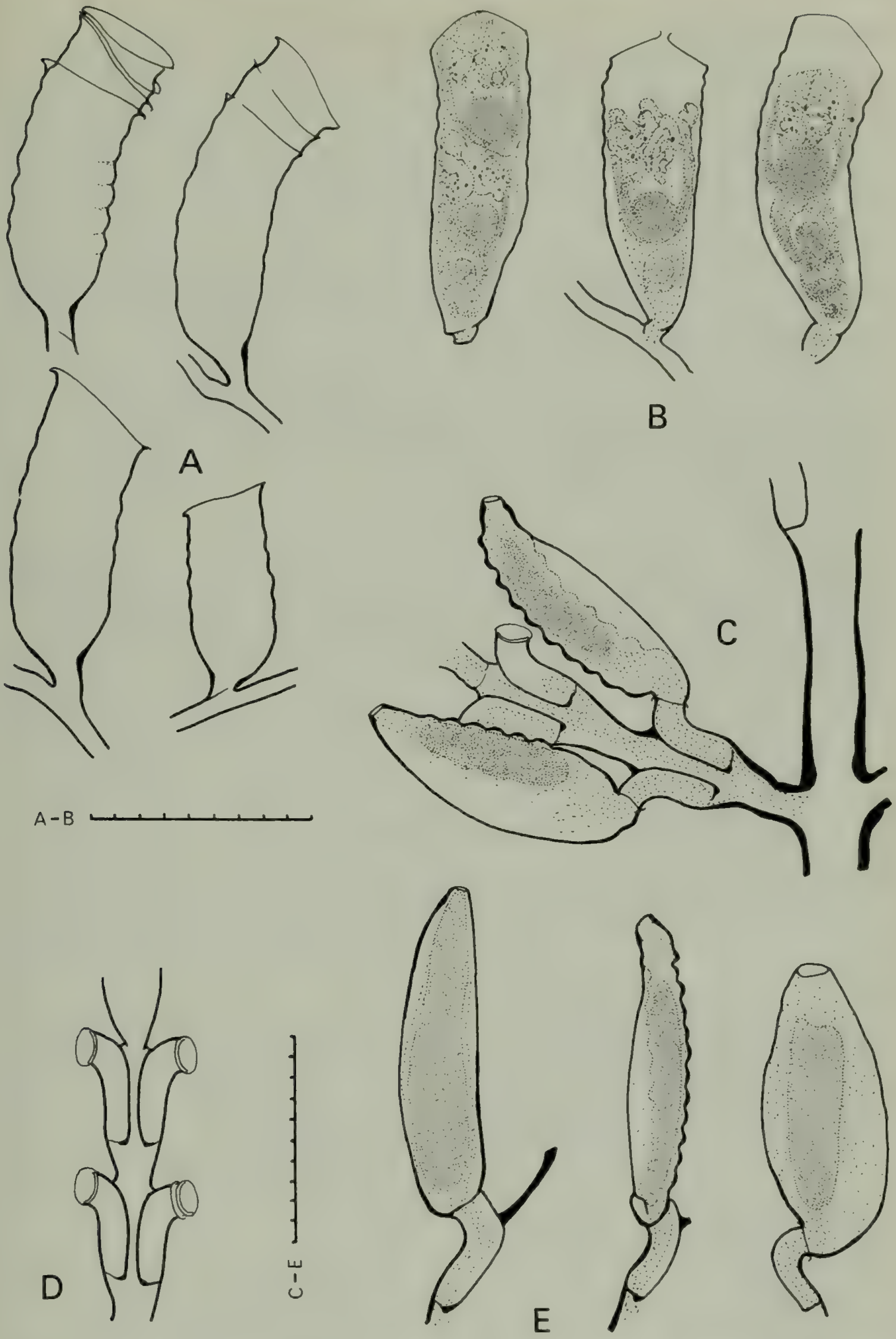

Fig. 3. *Hebella muscensis* sp. nov. A. Hydrothecae. B. Gonothecae containing medusa-buds. *Synthecium patulum*. C. Part of stem with a pair of gonothecae in narrow view. D. Part of hydrocladium. E. Gonothecae: a smooth one in narrow view, an annulated one in narrow view and a smooth one in broad view.

Scale in mm/10.

Measurements (mm)

Stem, internode length	0,41–0,74
Hydrotheca, length abcauline	0,43–0,53
length adcauline, adnate part	0,30–0,33
length adcauline, free part	0,30–0,38
diameter at margin	0,35–0,41

Remarks

H. corrugata has been reported from the western Indian Ocean from Natal to S.E. Madagascar (Gravier 1970). This record extends the range further north. The gonophores still await discovery.

Hincksella cylindrica pusilla Ritchie, 1910

Sertularella cylindrica var. *pusilla* Ritchie, 1910: 817, pl. 77 (fig. 9).
Hincksella cylindrica pusilla: Millard, 1964: 22, fig. 6A–D.
Cyclonia pusilla: Hirohito, 1969: 16, fig. 12.

Description

Stems normally unbranched, but one with a single lateral branch. Hydrotheca with a larger proportion adnate than the South African material described by Millard (1964), but otherwise very similar. Empty gonothecae present, arising from within hydrothecae, elongated and tapering distally.

Measurements (mm)

Stem, internode length	0,26–0,59
Hydrotheca, length abcauline	0,35–0,54
length adcauline, adnate part	0,15–0,34
length adcauline, free part	0,28–0,41
diameter at margin	0,12–0,27
Gonotheca, length from hydrothecal margin	0,57–0,77
maximum diameter	0,22–0,35

Remarks

This is the first discovery of gonophores in African material of the subspecies, and the shape is similar to that of the male gonophores described by Hirohito from Japan.

Synthecium patulum (Busk, 1852)

Fig. 3C–E

Synthecium orthogonia: Bale, 1888: 767, pl. 17 (figs 1–5).
Synthecium campylocarpum Allman, 1888: 78, pl. 37 (fig. 1).
Synthecium patulum: Billard, 1925: 125, figs 2–3. Millard & Bouillon, 1973: 64, fig. 8J.

Description

Pinnate stems reaching 2,0 cm, with 1–3 pairs of hydrothecae between successive pairs of hydrocladia.

Gonothecae arising from within hydrothecae on stem or hydrocladia and rather different in appearance from those described in 1973, being longer and more compressed. The transverse annulations, which number up to 11, are restricted to the centre region and are visible only in side view unless the gonotheca is empty, when the appearance is similar to Bale's diagram (1888: pl. 17 (fig. 5)). Within the same colony are gonothecae which have no annulations at all and are completely smooth. All gonothecae are male.

Measurements (mm)

Hydrotheca, length abcauline	0,36–0,50
length adcauline, adnate part	0,48–0,63
length adcauline, free part..	0,08–0,20
diameter at margin	0,17–0,22
Gonotheca, length	1,38–1,84
breadth	0,56–0,74
thickness	0,20–0,41

Remarks

Although the gonothecae are more compressed than any previously illustrated for *S. patulum* or its synonyms, we do not feel justified in creating a new species for what is probably a variable feature. It is possible that the shorter and fatter gonothecae illustrated in 1973 were female.

Family **Sertulariidae**

Dynamena obliqua Lamouroux, 1816

Pasythea quadridentata **var.** ***balei*** **Billard, 1907: 355, fig. 6.**
Dynamena obliqua: **Millard, 1958: 184, fig. 6A.**

Description

Stems reaching 6,6 mm, most of them with hydrothecal pairs ungrouped, some of them with one or two groups of two pairs. Hydrothecae smaller than those reported from Moçambique (Billard 1907) and from South Africa (Millard 1958), but shape very similar. Internal teeth present in most hydrothecae, one adcauline and two latero-abcauline.

Measurements (mm)

Hydrotheca, length abcauline	0,20–0,24
length adcauline, adnate part	0,20–0,24
length adcauline, free part..	0,12–0,14
diameter at mouth	0,07–0,08

Sertularella diaphana (Allman, 1886)

Thuiaria diaphana Allman, 1886: 145, pl. 18 (figs 1–3).
Sertularella diaphana: Billard, 1925: 157, figs 22–24, pl. 7 (figs 12–14). Millard, 1958: 188, fig. 7C–D.

Description

This stem is unusual in that it rotates through 90° half-way up. Both stem and hydrocladia are more slender than the South African material (Millard 1958) and are close to Billard's var. *delicata* (1925). The hydrocladia have only two or three hydrothecae to an internode.

Remarks

This species is known from the east coast of Africa, Mauritius and Madagascar, so its presence in the Seychelles is not unexpected.

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Family Nuculanidae

Nuculana (*Lembulus*) *bicuspidata* (Gould, 1845)

Figs 14–15A

Nucula (*Leda*) *bicuspidata* Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (figs 8a–b).
Nucula largillierti Philippi, 1861: 87
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

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(*continued inside back cover*)

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THERMALLY ANOMALOUS LATE PLEISTOCENE MOLLUSCS FROM THE SOUTH-WESTERN CAPE PROVINCE, SOUTH AFRICA

By

ANTHONY J. TANKARD

Cape Town Kaapstad

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By

ANTHONY J. TANKARD

South African Museum, Cape Town

(With 3 figures and 2 tables)

[*MS. accepted 29 May 1975*]

ABSTRACT

Numerous exposures of Late Pleistocene marine sediments occur on the west and south coasts of the Cape Province. The mollusc fauna, which includes some 124 species, only 3 of which are extinct, lived in sediments deposited during the last interglacial. Two broad and contemporaneous facies are recognized: a cool-water open-coast facies, and a warm-water estuarine-lagoonal facies. Whereas the open-coast facies is characterized by molluscs which presently live on the adjacent coast, the estuarine-lagoonal facies regularly contains tropical species which lived far south of their known present-day geographic ranges. Differences in distribution between the fossil warm-water molluscs and their present-day temperature-sensitive counterparts have been used to interpret Late Pleistocene climatic change in the south-western Cape. These deposits are correlated with the Mediterranean Eutyrrhenian.

CONTENTS

PAGE
Introduction 17
Geologic Setting 18
Methods 20
Palaeoecology 21
  Population Dynamics 25
  Predation 29
  Teratological Specimens 31
  Depth 31
  Temperature 32
  Summary 37
Palaeoclimatic Interpretation 38
  Review of Present Climate and Hydrology . . . 38
  Late Pleistocene Climate 40
Discussion 41
Acknowledgements 43
References 43

INTRODUCTION

Isolated fossiliferous, marine sediments occur on the wave-cut platform and in the sheltered Late Pleistocene embayments from Elands Bay on the west coast to Knysna on the south coast. The fossils occur in unconsolidated quartzose and shelly quartzose sands. The invertebrate fauna is essentially modern in composition and comprises some 150 species which today live in shallow-water environments. Only three of the mollusc species from the west

Ann. S. Afr. Mus. **69** (2), 1975: 17–45, 3 figs., 2 tables

coast deposits are not known to be living today. In so far as most of these taxa are still living, and are inhabitants of shallow water, they provide ideal material for a palaeoecological study.

The Late Pleistocene fauna of the west coast is broadly divisible into two distinct, but contemporaneous, ecologic zones. These are, firstly, a cool-water, open-coast facies characterized by rocky shore and sandy beach assemblages, and secondly, a warm-water, sheltered embayment facies (estuaries and lagoons). Whereas the open-coast facies is laterally continuous, the sheltered embayment facies is restricted in distribution. The open-coast facies is characterized by molluscs which commonly inhabit the present coast. A striking feature of the estuarine-lagoonal facies is the association of extant and extralimital thermophilic species. ('Thermophilic' and 'extralimital' imply species which occur outside their normal spawning range.) Examination of their present latitudinal ranges indicates that a significantly warmer hydroclimate prevailed when those species were common along the south-western Cape coast. In attempting to reconstruct the palaeoenvironment, a detailed examination of a south coast assemblage is necessary. The fossiliferous deposits at Knysna are therefore included in the study.

Late Pleistocene faunas of open-coast and sheltered-embayment aspects from southern California are similarly distinctive. Nearly all the dominant species also inhabit the adjacent coast. But the sheltered embayments also contain a high proportion of thermophilic molluscs which are found far north of their present-day geographic range end-points. Several authors have used these anomalies as a key to Late Pleistocene climatic interpretation (Valentine 1955, 1957, 1961; Valentine & Meade 1961; Addicott & Emerson 1959; Emerson & Chase 1959; Kern 1971). Valentine (1955) explained the diverse nature of the fauna by changes in intensity of the oceanic circulation and upwelling, while the water of the embayments was heated by increased solar radiation. A recent alternative explanation suggests that the larvae of tropical molluscs were transported into the cooler areas by periodic local and temporary current changes, and that they became only temporary, non-breeding, members of the community (Zinsmeister 1974).

The south-western Cape Province, with its extensive Late Pleistocene fossiliferous deposits, and its complex present-day ocean current systems, is well placed to make a contribution to the knowledge of Late Pleistocene hydroclimates. The purpose of this paper is to describe the mollusc fauna, particularly between Ysterfontein and Elands Bay, and to examine their palaeoenvironmental significance. The taxonomy of some of these molluscs appears elsewhere (Kilburn & Tankard, in press).

GEOLOGIC SETTING

The Pleistocene epoch was characterized by the waxing and waning of continental ice sheets with sea level oscillating in sympathy. Relative movement of sea level is shown by the emerged wave-cut platforms, stranded beaches,

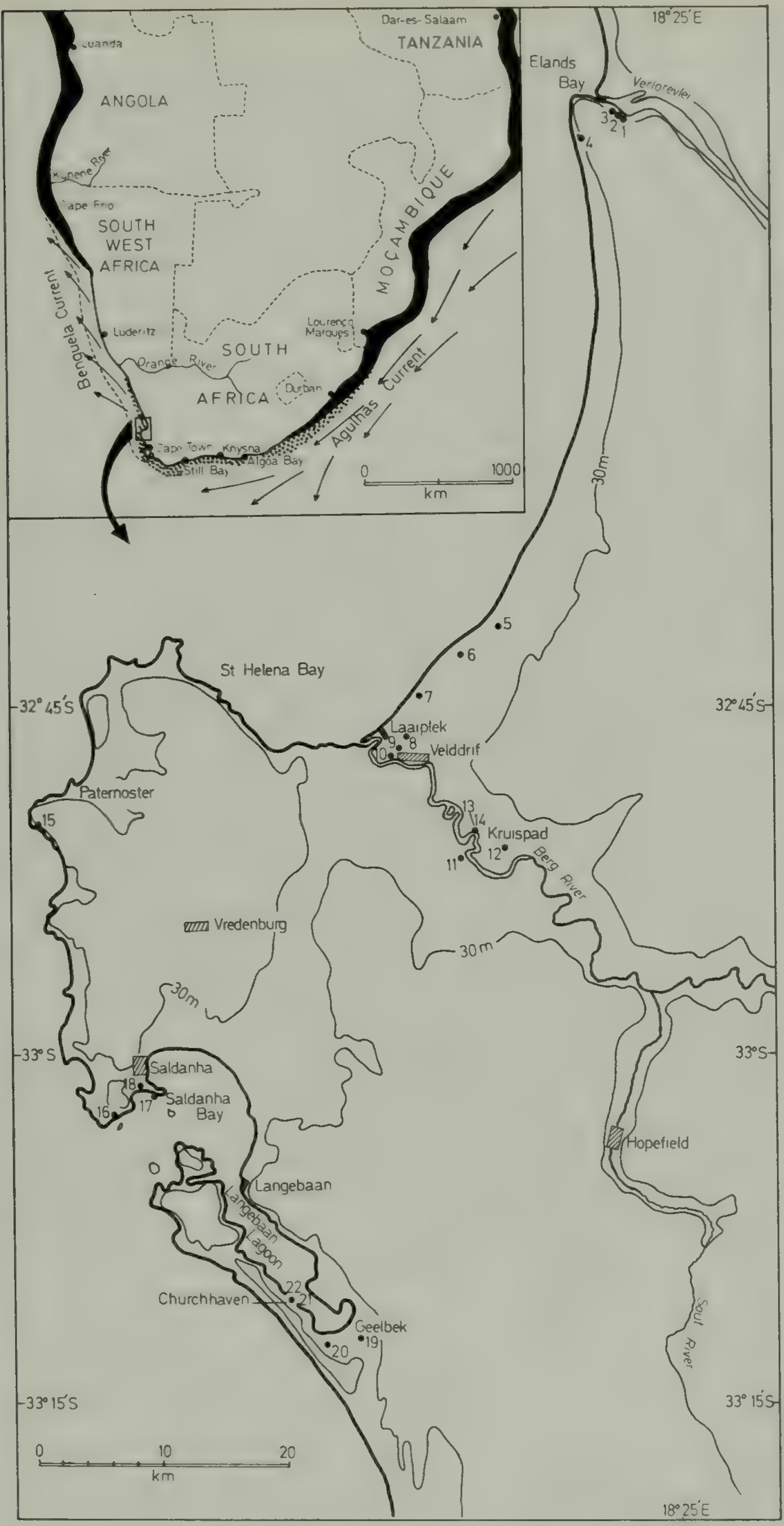

Fig. 1. Locality map. The insert (partly after Boss 1969) shows the distribution of present-day coastal forms: black = tropical; stippled = warm–temperate; area bounded by broken line on west coast = cold water fauna.

and marine terraces. Research on Barbados has suggested the existence of three transgressions in the last interglacial (Eem): +6 m (BI) at 122 ka (i.e. 122 000 years ago); −13 m (BII) at 103 ka; −13 m (BIII) at 82 ka (Broecker *et al.* 1968). These three peaks are confirmed by oxygen isotope studies of deep-sea cores (Shackleton & Opdyke 1973).

Along the west coast of South Africa a thin mantle of Late Pleistocene marine sediments overlies earlier Pleistocene, Tertiary, and pre-Tertiary rocks. On the granitic headlands between St. Helena Bay and Ysterfontein a narrow seaward-sloping wave-eroded platform is encountered. St. Helena Bay has formed on Malmesbury rock which weathers more rapidly than the granite and gives a negative relief. The open-coast fossil assemblages were collected from marine deposits overlying the granite platforms, and from exposures in the coastal flats bordering St. Helena Bay.

The last interglacial shorelines parallel the present coast very closely, with two exceptions. Whereas the present coastline is interrupted only by Saldanha Bay and its southerly offshoot, Langebaan Lagoon, the Late Pleistocene sea extended up the Berg River valley and along Verlorevlei to form two prominent estuaries. Verlorevlei is now separated from the sea by a bar of Palaeozoic sandstone at 1 m a.s.l. (above mean sea level). These sheltered Late Pleistocene estuaries and lagoons were of considerable palaeogeographic importance since all fossil sites within them contain a significant proportion of thermophilic mollusc species.

The greatest observed thickness of the open-coast facies exceeds 5 m at Velddrif; the greatest observed thickness of the estuarine facies is 2,2 m at Verlorevlei. The open-coast facies consists of medium-grained quartzose sand and comminuted shell. Frequently there are shell beds and banks with little detrital quartz, indicating a slow supply of detrital sediment. A series of emerged breaker-bars between Velddrif and Laaiplek parallel the modern coast. These are composed largely of shell material.

In all the sheltered embayments the fossils are found in fine sands. At Verlorevlei the marine horizon is overlain by coarse, poorly-sorted colluvium. At Churchhaven the marine sediments are carbonate cemented and form an erosional bench just above high-water level. Most of the sites examined, both open-coast and sheltered embayment, are covered with a veneer of wind-blown sand.

METHODS

The absolute density of fossil specimens of each molluscan species at any particular site is difficult to determine because of the sampling problems inherent on the size of the shell. For instance, '*Rissoa*' *capensis* is a small gastropod (usually less than 3 mm) and would frequently number in the hundreds from just 100 g of sediment, while the large (approximately 200 mm) *Panopea glycymeris* would occur at approximately 1 m intervals. Bearing in mind that the present study is a palaeoecological one, and that the larger molluscs have been better studied with respect to taxonomy and ecology, emphasis has in all cases been placed on the macro-molluscs. A further source of error arises from the differential fragmentation of shells. Bivalve shells are more easily broken than gastropod shells, and in the living assemblage they may have been far more abundant than the faunal list suggests. Table 1 should be taken only as an approximation to the original community structure.

The procedures adopted in drafting Table 1 are as follows:

1. It was desirable to sample as small an area as possible to obtain not only the absolute density of each species, but also to obtain restricted samples for size-frequency analyses. In most cases a quadrat size of 1 square metre has been found adequate, although quadrat size may have to be adjusted up or down depending upon the relative abundance of specimens.

2. For a shell to be counted as an individual it must be nearly complete, or so nearly so that the remainder could not be identified and counted separately. Left and right valves of each bivalve species were counted separately, and the highest count taken as the total number of individuals of that species in that quadrat.

3. Each species has been recorded in Table 1 as percentage frequencies in the sample where more than 50 individuals were counted. Where a total of less than 50 individuals were counted they are recorded in Table 1 as '×'.

No attempt has been made to relate species to sediment texture since every mollusc at some time must have been living among already dead and fragmented shells. The substrate would thus consist of quartzose sand and bioclastic material ranging in size from complete shells to finely comminuted fragments.

PALAEOECOLOGY

In this paper past extensions of tropical and subtropical mollusc geographic ranges are used as a basis for interpreting Late Pleistocene palaeotemperature changes. These inferences are based only on fossils of still extant species, and the assumption (Durham 1950) that stenothermal organisms are in general more critically limited by minimum temperatures than by maximum temperatures. The validity of such palaeotemperature inferences depends on the fossils being preserved in the sediments in which they once lived.

In describing the relationship between the fossils, after death, and the sedimentary environment, we define the following types of fossil assemblages:

1. Life assemblage: disturbance after death negligible (Hallam 1960).
2. Death assemblage:
   - (i) Indigenous: organic remains disturbed after death but not transported very far (Hallam 1960).
   - (ii) Transported: organic remains introduced from a neighbouring contemporaneous or older environment.
3. Mixed assemblage: this comprises any combinations of the above

TABLE 1

Distribution and Abundance (%) of Late Pleistocene Molluscs

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	*Lagoon Floor*	*Knysna*
GASTROPODA																								
Amblychilepas scutella (Gmelin)												< 1						< 1						< 1
Fissurella aperta (Sowerby)																					< 1			
F. mutabilis Sowerby												< 1	×					1,3	1,0					
Helcion pectunculus (Gmelin)															< 1	< 1								
Patella argenvillei Krauss															7,8	7,2								
P. barbara Linnaeus	2,0														7,4	< 1	×							
P. cochlear Born															2,0	2,6	×							
P. compressa Linnaeus									1,0						3,9	1,3		< 1						
P. granatina Linnaeus			< 1						1,0	×					8,3	2,0								
P. granularis Linnaeus															4,9	10,5								
P. longicostata Lamarck																		< 1						
P. miniata Born						×			< 1						< 1									
Cantharidus suarezensis fultoni (Sowerby)																								9,8
Gibbula cicer (Menke)												< 1												
Minolia sp.																								< 1
Oxystele trigina (Chemnitz)			< 1																		< 1			
O. variegata (Anton)			1,4													< 1		15,7		9,4	2,7	2,4		
Monilea alexandria (Tomlin)																								1,8
Solariella sp.																						1,0		
Pseudostomatella orbiculata (A. Adams)																								< 1
Turbo cidaris Gmelin															< 1	< 1								
T. sarmaticus Linnaeus																								< 1
Littorina knysnaensis Philippi			< 1													2,0		4,6						< 1
Alvania alfredensis Bartsch																		< 1						
Coriandria cf. *halia* (Bartsch)																					< 1			
'*Rissoa*' *algoensis* Thiele								×																
'*Rissoa*' cf. *capensis* Sowerby			×	×				×			×	×						×			×	×		×
Turritella capensis Krauss								×	< 1		18,0								2,0			1,7		2,6
T. carinifera Lamarck																			18,4	7,1		6,6		
T. sanguinea Reeve												10,3	×											
Cerithium kochi Philippi																								3,7
C. scabridum rufonodulosum E. A. Smith																								16,3
Diala infrasulcata Sowerby																								< 1
Alaba pinnae Bartsch																								< 1
Calyptraea chinensis (Linnaeus)							×		< 1					×				< 1				1,0		
Crepidula aculeata (Gmelin)					1,3							< 1	×	×		3,3			< 1			1,0		
C. porcellana Lamarck						×		×	< 1			< 1		×	1,5	< 1	×			1,2	1,9			< 1
C. capensis praerugulosa Kilburn & Tankard			< 1	×	46,7				18,1			< 1			10,8									
Cypraea algoensis Gray																< 1								
Natica genuana Reeve									< 1		4,0	< 1							1,0	12,9				< 1

Argobuccinum argus (Gmelin)	< 1		2,7				< 1						5,4	[illegible]	×	< 1						
Cymatium dolarium (Linnaeus)	< 1																					
Thais cingulata (Linnaeus)				×									1,5	3,3								
T. dubia (Krauss)																< 1			< 1			< 1
T. squamosa (Lamarck)			1,3	×			< 1	×		< 1		×	12,3	19,6	×	1,3						
Burnupena papyracea papyracea (Röding)					×		< 1							35,9	×	7,8		10,6	< 1			
B.p. cincta (Bruguière)	< 1									< 1			19,1				2,0		1,0	3,3		
B. digitalis Meuschen			8,0	×	×	×	1,0	×					< 1			1,3	< 1	1,2	5,5	1,0		
B. laevissima (Gmelin)			5,3	×	×		10,5									< 1	< 1					
Nassarius analogicus Sowerby		×					< 1															
N. kochianus (Dunker)										< 1												
N. kraussianus (Dunker)						×																1,6
N. plicatellus (A. Adams)																	4,1	2,3	5,1	4,1		
N. scopularcus Barnard	4,7	×					< 1	×	30,0	11,5	×											
N. speciosus A. Adams							< 1									< 1	1,0		< 1	1,0		
Fasciolaria lugubris Reeve							< 1							< 1		< 1	< 1	3,5	< 1	2,5		
Marginella capensis Krauss		×				×	< 1	×		5,8	×					2,0	3,0	3,5		1,0		
M. piperata Hinds													< 1	< 1								
Mitra aerumnosa Melvill														< 1								
Vexillum capense (Reeve)														< 1								
Cythara amplexa (Gould)										< 1						< 1						
Clionella sinuata (Born)													1,0	< 1		19,0	3,0	10,6	2,3	4,1		
Conus scitulus algoensis Sowerby													6,4	1,3	×							
Syrnola aganea (Bartsch)																						< 1
Turbonilla kraussi Clessin										< 1												
Turbonilla sp.																						< 1
Pupa daviesi Kilburn & Tankard																						< 1
Ringicula turtoni Bartsch																						< 1
Philine aperta (Linnaeus)																						< 1
Cylichna tubulosa Gould										< 1												
Bullaria ampulla (Linnaeus)																						1,0
Atys cylindrica Sowerby																						< 1
Siphonaria aspera Krauss													1,5	1,3		5,2						
S. capensis Quoy & Gaimard	< 1																1,0		1,6	1,7		
BIVALVIA																						
Nuculana bicuspidata (Gould)										3,2												
Aulacomya ater (Molina)	< 1		1,3	×	×								2,9	< 1						1,0		
Perna perna (Linnaeus)		×	1,3	×			1,0	×								1,3						
Choromytilus meridionalis (Krauss)				×											×				< 1			
Chlamys tinctus (Reeve)																						< 1
Pecten sulcicostata Sowerby																						< 1
Lima fragilis (Chemnitz)																						< 1
L. rotunda Sowerby																						< 1
Ostrea atherstonei Newton														< 1			5,1	7,1	< 1	5,0	> 99	
O. stentina Ranson	2,7																					
O. algoensis Sowerby										9,6	×											< 1

TABLE 1 (*contd.*)

Distribution and Abundance (%) of Late Pleistocene Molluscs

BIVALVIA (*contd.*)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	*Lagoon Floor*	*Knysna*
Loripes liratula (Sowerby)	9,0	20,0	26,4								8,0	15,4	×	×					20,4	14,1	< 1	4,1		57,5
Anodontia edentula (Linnaeus)																								1,4
Felania diaphana (Gmelin)																								< 1
F. subradiata Sowerby																					1,0			
Erycina subradiata (Gould)								×																
Lasaea rubra Montagu			< 1																		1,0	1,0		
Mysella convexa (Gould)			< 1															< 1						
Tellimya trigona Barnard												< 1						26,1						
Tellimya sp.								×																
Cardita sp.												< 1												
Parvicardium turtoni (Sowerby)																								< 1
Mactra glabrata Linnaeus														×					4,1			11,4		
M. ovalina Lamarck																			1,0	1,2	2,3	1,7		1,2
Scissodesma spengleri (Linnaeus)						×	×																	
Lutraria lutraria (Linnaeus)					2,7	×	×		11,4	×		1,3												
Lutraria sp.																								< 1
Solen capensis Fischer			1,4	×					< 1		2,0	1,9		×				1,3	< 1	1,2	< 1			< 1
Phaxas pellucidus (Pennant)									< 1															
Tellina ponsonbyi Sowerby																					< 1			
T. madagascariensis Gmelin	6,0	10,0	8,1						< 1										10,2	9,4	23,4	3,3		< 1
T. trilatera Gmelin					12,0														< 1					
T. gilchristi Sowerby												< 1						< 1			< 1			
Macoma crawfordi Sowerby				×														< 1						
M. litoralis (Krauss)																								< 1
M. tricostata (Römer)	2,0	3,0	< 1																					
Gastrana matadoa (Gmelin)			4,1											×					1,0			9,1	< 1	< 1
G. fibrosa Kilburn & Tankard																		1,3						
Leporimetis hanleyi (Dunker)											2,0	1,0								< 1				< 1
Donax serra (Chemnitz)					2,7	×			1,0										< 1	< 1	3,1			
D. sanctuarium Kilburn & Tankard																					1,0			
Psammotellina capensis Sowerby				×				×			34,0										1,0			
Theora alfredensis Bartsch												< 1										1,0		< 1
Venus verrucosa Linnaeus			< 1		2,7				< 1	×									16,3	3,5		18,4		< 1
Tivela tomlini Haughton																					1,7			
Dosinia lupinus Linnaeus	81,0	67,0	50,0	×							2,0	18,6	×						1,0		39,1	9,9		< 1
D. hepatica (Lamarck)																								< 1
Venerupis senegalensis Gmelin			< 1	×	12,0	×			55,0	×		12,8	×	×	1,0			3,3			3,5	1,7		1,0
V. dura Gmelin			< 1									6,4	×						4,1	1,2				< 1
Panopea glycymeris (Born)												1,3												
Total number individuals	100	100	148		75				105		50	156			204	153		153	98	85	256	121		492
% thermophilic species	60,0	75,0	26,1								22,2	25,8	20,0	33,0				6,9	26,9	31,6	22,6	25,9		12,8
% thermophilic individuals	17,0	33,0	41,9								20,0	42,9						—	45,9	32,9	28,1	35,5		60,4

possibilities, and is the general case (Hallam 1960). The status of this assemblage is clarified by describing it, for instance, as a mixed life and indigenous death assemblage. In the present study this is the commonest case.

POPULATION DYNAMICS

Boucot (1953), Olson (1957), Craig & Hallam (1963), and Craig & Oertel (1966) have attempted to discriminate between life and indigenous death assemblages on the one hand and transported death assemblages on the other, by using size-frequency distributions. According to Boucot an indigenous death assemblage is characterized by a positively skewed distribution (large number of small forms), while negative skewness or a normal distribution characterizes the transported death assemblage. He suggested that negative skewness resulted from winnowing of the smaller shells. Craig & Oertel (1966) question this and maintain that the shape of the size-frequency distribution in a fossil population depends principally upon the growth-rate and mortality-rate of the relevant species. In this way negative skewness could arise from a decreasing growth-rate with constant mortality-rate which would concentrate the older age-classes in a few size-classes. Craig and Oertel suggest the following options:

Growth-rate	*Mortality-rate*	*Size-frequency distribution*
decreasing	constant	negative skewness
constant	decreasing	positive skewness
constant	increasing	flattening of curve, possibly negative skewness
constant	constant	mirror image of living population by dead population

Growth-rate and mortality-rate complement each other when one decreases and the other increases, but cancel each other if both increase or decrease.

Higher mortality-rates which favour large populations may result from a fluctuating environment (Valentine 1971). Mortality is affected by nutrients, temperature, and salinity changes. In general, invertebrates have higher mortality-rates in the early stages of life, but the rate may be lower in some species than others (Craig & Oertel 1966). Environmental conditions in estuaries and lagoons would be expected to fluctuate widely and rapidly. They would be expected to show a variable salinity range due to evaporation and influx of fresh water, and a high diurnal temperature range. Furthermore, seasonal upwelling of cold water along the Cape west coast leads to marked instability of the environment on the open coast too.

Although growth-rate is an important factor in this type of study, it is one of the attributes about which there is little information. There is evidence, however, that most bivalves maintain a slightly decreasing, but nearly linear, growth-rate throughout life (Craig & Oertel 1966). This has been shown to be the case for *Cardium edule*, *Tapes japonica*, *Dosinia exolata*, and *Venus striatula* (Kristensen 1959; Wilbur & Yonge 1964).

The most likely effect of the unstable environmental characteristics of the west and south coasts of the Cape would be a high mortality-rate among the juvenile molluscs. Assuming a constant growth-rate for the bivalves, the interplay of mortality-rate and growth-rate should lead to a positively skewed size-frequency distribution for a life assemblage, or an indigenous death assemblage.

Besides the effect of growth-rate and mortality-rate on the shape of the histogram, the assemblage may be affected by post-death mechanical change such as sorting or winnowing by currents (Boucot 1953) and selective fragmentation, and solution of the smaller or thinner shells. Experience with the west coast fossils shows that crushing and fracturing is of primary importance, and affects the bivalves more than the gastropods.

The large number of fragmented shells in both the open-coast facies and estuarine-lagoonal facies sediments suggests death assemblages that have undergone considerable modification by wave-action. Whereas the open-coast bivalves are usually disarticulated, those in the estuarine-lagoonal sediments show a high degree of articulation. These sheltered embayment sites contain epifaunal and infaunal molluscs, some of which are preserved in their living positions. Size-frequency distributions for some of the bivalves are shown in Figure 2. Since the warm-water element inhabited the Late Pleistocene lagoons and estuaries, samples from those environments have been analysed in most detail.

A single sample from a known high-energy open-coast site was examined in detail. Figure 2A shows the size-frequency distribution for *Venerupis senegalensis* from the Velddrif site. The field-setting suggests a transported death assemblage in which vigorous wave-action piled shell debris up to form a breaker-bar. In these deposits the thinner shells have generally been fragmented. The *V. senegalensis* population is composed of thick-shelled forms. Its estuarine ecomorph, on the other hand, has a thinner shell and is of more constant morphology. The Velddrif *V. senegalensis* shows marked negative skewness (−0,82). It has an articulation ratio less than 0,05. Articulation ratio is defined as the ratio of complete shells/$\frac{1}{2}$ (RV+LV).

Size-frequency distributions of bivalves from the estuarine-lagoonal facies differ from the pattern of the Velddrif example. *Tellina madagascariensis* from Verlorevlei (Fig. 2C) and Churchhaven (Fig. 2H) tends to have a flattened histogram. The Verlorevlei *Tellina* has a size-peak at 64–66 mm, and the Churchhaven specimens at 56–60 mm. While the narrower size range of the Verlorevlei material (50–86 mm) suggests a transported death assemblage, the greater range of the Churchhaven material (16–74 mm; more juveniles) suggests an indigenous death assemblage. That this argument can be misleading is shown by their articulation ratios of 1,46 and 0,47 respectively. At both of these localities *T. madagascariensis* is associated with comminuted shells and disarticulated valves of other species. *T. madagascariensis* at Verlorevlei was observed in a nearly horizontal attitude as were the other bivalves. But whereas

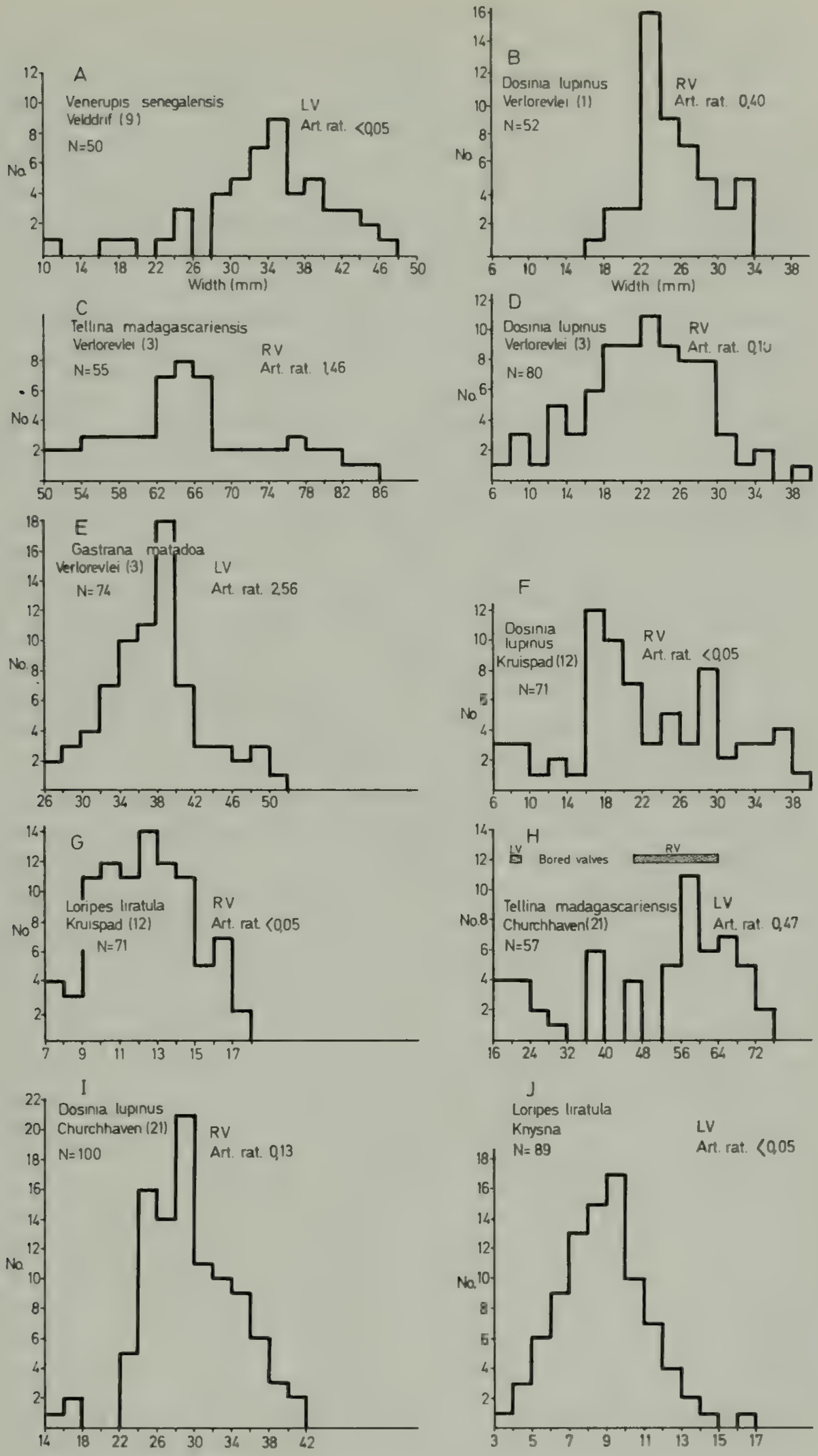

Fig. 2. Size-frequency distribution of selected bivalve shells.

most bivalves burrow with the shell vertical, *Tellina* burrows rapidly and settles in a horizontal position. For this reason the posterior end of the shell is strongly flexed to the right so as to broaden the radius of curvature of the siphons to minimize the current flow constriction. In a small quadrat at Verlorevlei 29 articulated shells were observed. Of these 26 had the right valve uppermost, i.e. flexure upwards, and with the posterior end slightly raised. Many of the *T. madagascariensis* shells still had the ligamental material attached across both valves as a powdery residue. Clearly these animals must have died in their life positions where the weight of sediment prevented opening of the shells after relaxation of the adductor muscles. If they had opened after death and subsequently closed again due to increased sediment load, the ligament would have broken.

At Verlorevlei the *T. madagascariensis* (site 3) size-frequency distribution can be compared with those of *Gastrana matadoa* and *Dosinia lupinus* (Fig. 2B, D, E). *Dosinia lupinus* at site 1 (Fig. 2B) has a positively skewed (+0,37) histogram with an articulation ratio of 0,40. The field occurrence suggests that reworking of the sediment has taken place, although the shells are still situated close to their original life habitat. Although the articulation ratio is high, relative displacement of each valve is common. At site 3 the *D. lupinus* histogram is bell-shaped (Fig. 2D). Here the articulation ratio is only 0,10. The bell-shaped distribution suggests less winnowing of the small specimens. Both *D. lupinus* populations peak at 22–24 mm. From site 1 to site 3 at Verlorevlei there is a tendency for a greater spread of size-ranges of *D. lupinus*: 16–34 mm at site 1 and 6–40 mm at site 3. Conceivably the histogram for *D. lupinus* (site 1) was originally bell-shaped but winnowing may have removed the smaller sizes. This is borne out to an extent by the increase in relative proportions of *Loripes liratula* in the assemblage, from 9 per cent at site 1 to 26,4 per cent at site 3. The size-range of *L. liratula* 3–17 mm (Fig. 2G, J) coincides with the juvenile fraction of *D. lupinus*. Because of the close similarity in shape of *D. lupinus* and *L. liratula*, equal-size specimens of each species would be expected to be hydraulically equivalent.

The size-frequency distribution of *Dosinia lupinus* at Churchhaven has a tail towards the larger specimens (Fig. 2I), suggesting winnowing. It has a narrow size-range, 14–42 mm, and peaks at 28–30 mm. The low articulation ratio (0,13) suggests reworking.

At Kruispad the *Dosinia lupinus* population again has a wide size-range, 6–40 mm (Fig. 2F), but an articulation ratio less than 0,05. Furthermore, the histogram has two peaks, at 16–18 mm and 28–30 mm. The bimodal distribution could be explained by extinction of one living population, followed by fresh recruitment when environmental conditions improved. The site is 15 km up the Berg River and could possibly have been influenced by sudden influxes of fresh water. But *Loripes liratula* at this site appears to represent a single population: the histogram is bell-shaped and peaks at 12–13 mm. Its low articulation ratio (< 0,05) may be meaningless since this species does not have prominent dentition, and seldom in this study were articulated valves encountered. For example, *Loripes liratula* from Knysna has an articulation ratio less than 0,05 although juveniles dominate. Craig (1967) found that of five species he examined, only *Divaricella quadrisulcata* tended toward a normal distribution. (*Divaricella* and *Loripes* are both Lucinidae.)

Gastrana matadoa (Fig. 2E) at Verlorevlei is positively skewed and has a high articulation ratio (2,56). This high articulation ratio, compared with that of *Dosinia lupinus* from the same site, could be due to the more robust dentition of the former, but the greater proportion of juveniles of *G. matadoa* suggests it probably is closer to a life assemblage.

In general, the sign of skewness alone as used by Boucot (1953) is insufficient to distinguish between indigenous and transported death assemblages. The field-setting shows the Velddrif breaker-bar deposit to contain a transported death assemblage. It has strong negative skewness and a low articulation ratio. This tail towards the left has been produced by winnowing of the finer fractions, and effectively displacing the mode towards the coarser size-grades. The other size-frequency distributions are suggestive of indigenous death assemblages which have in most cases been slightly reworked. In Figure 2B the lack of juveniles of *Dosinia lupinus* coincides with low numbers of the hydraulically equivalent *Loripes liratula*.

Other indications that the shells are found in the sediment in which they once lived include relatively high articulation ratios of the larger shells. Smaller shells, e.g. *Loripes liratula*, tend to have weaker hinge attachments, while juveniles of other species may have been subjected to predation. *Tellina madagascariensis* at Verlorevlei appears to be in a life orientation, and also has the ligamental material still attached. At Kruispad a bed contains *Panopea glycymeris* still in the life orientation. The shells were all articulated, all posterior end upwards, and all on the same horizontal plane, i.e. they had all burrowed a siphon-length below the sediment-water interface. At most sites, left and right valves were present in equal proportions.

In conclusion, the field-setting shows that open-coast assemblages are all transported death assemblages, but transportation has been only local. The faunas of the sheltered environments are mixed life and indigenous death assemblages. Taken as a whole the fauna of the open-coast facies and the estuarine-lagoonal facies are consistent with the inferred Late Pleistocene environments.

PREDATION

Many of the bivalve shells are punctured by countersunk borings, 1–2 mm in diameter, made by predatory gastropods. The bored bivalves include: *Dosinia lupinus*, *Tellina madagascariensis*, *Gastrana matadoa*, *Venerupis senegalensis*, *Venerupis dura*, and *Ostrea algoensis*. *Crepidula capensis* and *Natica genuana* were the most frequently bored gastropods.

At Churchhaven 17 per cent of *Dosinia lupinus* and 17 per cent of *Tellina* *madagascariensis* were bored. In the case of the former an equal number of right and left valves were bored, as would be expected in view of the fact that it burrows in a vertical position. Analysis of predation on *T. madagascariensis* reveals a very different pattern. Successfully bored valves fell into two size-classes (Fig. 2H). The first group comprised juveniles with a size range 20–22 mm, and the second group adults with a size range 46–64 mm. Only right valves of adults were bored, which is to be expected because this species lives buried in sediment in a horizontal position and with right valve uppermost. Craig (1967) found that the right valve of *Tellina radiata* was also preferentially bored. The second group of *T. madagascariensis* comprised juveniles in which left valves were preferentially bored, although a few right valves were also bored. The preferential boring of juvenile left valves could also be the result of the burrowing characteristics. *Tellina* is a rapid burrower (Stanley 1970). Depth of burrowing would be controlled by length of the siphons, and for this reason the juveniles would presumably live at shallower depths than the adults and would possibly burrow more slowly. Subsequent current scour would possibly reach only the juveniles and flip them over to leave them left valve uppermost. This also suggests that, besides predation, the juvenile bivalves would be more susceptible to environmental changes since they live closer to the surface.

Most of the bored bivalve shells have only one hole, which is not surprising since only one puncture is necessary to kill the animal. In a few cases two holes per shell were encountered. As far as *Tellina madagascariensis* is concerned the borings occur most frequently in the antero-dorsal half of the shell (Fig. 3). It was also observed that all bored specimens of *T. madagascariensis* at Churchhaven consisted of separate valves, while four bored articulated shells of *Dosinia lupinus* were observed.

Of the gastropods, *Crepidula capensis* was the most extensively bored. Again there was usually only one hole per shell, although up to three were recorded. The reason why *Crepidula capensis* is so susceptible to predation is because it lives exposed at the surface where it is an easy prey. Unlike the bivalves, *Crepidula* does not appear to have any preferred area for boring (Fig. 3).

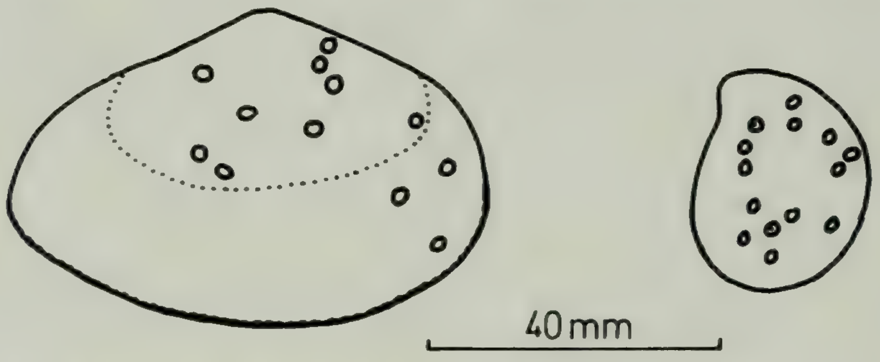

Fig. 3. Predation: distribution of borings on *Tellina madagascariensis* (left), and *Crepidula capensis* (right).

Crepidula capensis from the shell beds north of Laaiplek have smaller bored holes (less than 1 mm) than other *C. capensis* or the bivalves.

It is difficult to isolate the species that would have been the predator, although it seems probable that the borings were made by a gastropod. The most likely predator would appear to be the buccinid *Burnupena papyracea*. Where many bivalves were found to be bored at Churchhaven, *B. papyracea* was very prominent. At Verlorevlei there was a total absence of *B. papyracea* and no sign of predation on bivalves.

TERATOLOGICAL SPECIMENS

Teratological specimens are those that are outside the normal range of variation of a species (Ager 1963). At most sites an occasional aberrant form was observed, and it was found generally that *Gastrana matadoa* was the most susceptible to damage during life. This was very apparent at Verlorevlei (site 3) where 27 per cent of *G. matadoa* were in some way deformed, compared with less than 2 per cent for *Tellina madagascariensis*. Perhaps this reflects the degree of adaption of *G matadoa* to its niche, and that the environment at Verlorevlei in particular did not favour this species.

DEPTH

Regional geomorphic analysis suggests that the depth of water reflected in the strata of all open-coast and sheltered embayment sites examined could not have exceeded 5 m. The Late Pleistocene estuarine-lagoonal facies is dominated by intertidal deposits, and the open-coast facies by beach deposits. At Velddrif there is a good exposure of a breaker-bar with a washover-fan the top of which is probably a close approximation to high water spring tide. At Churchhaven and Kraalbaai *Callianassa* burrows and crab-burrows are still preserved, indicating an intertidal or shallow subtidal environment. The ostracod fauna, too, is indicative of intertidal conditions.

Very few of the 124 species listed in Table 1 suggest water depths greater than 25 m. Most of these species live today in intertidal and the uppermost sublittoral zones. Less than 4 per cent of the fauna lives today in water deeper than 25 m.

Of the open-coast assemblages *Nassarius speciosus* is today usually dredged, although it is sometimes found intertidally. No more than a few isolated shells were found. *Erycina subradiata* has been encountered at 26 m (Barnard 1964). Other species have a wide depth range although they are common in the intertidal zone. Nearly all species of *Patella* encountered at open-coast sites are intertidal. Only *P. miniata*, *P. tabularis*, *P. compressa* are infratidal (Branch 1971). Other intertidal molluscs include: *Littorina knysnaensis* (above HWN), *Marginella capensis* (low tide down), *Bullia digitalis* (follows the tide), *B. laevissima*, *Thais cingulata*, *Burnupena papyracea* (below mid-tide), *Perna perna* (mid-tide), *Aulacomya ater* (mid-tide to low tide on rocky shores), *Choromytilus meridionalis*, *Dosinia lupinus*, *Donax serra* (burrows in surf beaches below mid-tide), *Venus verrucosa* (found on the surface at mid-tide). Depth ranges are given by Day (1969).

Of the estuarine-lagoonal facies molluscs *Ostrea algoensis* prefers depths of 25–200 m, *Tellina ponsonbyi* prefers off-shore waters to depths of 95 m, and *Theora alfredensis* has been dredged from depths below 70 m (Barnard 1964). *Ostrea algoensis* and *Theora alfredensis* are common in this facies. Only one *Tellina ponsonbyi* valve was found at Churchhaven, suggesting that this specimen strayed into shallow water.

Most of the sheltered-embayment molluscs prefer very shallow or intertidal water. These include the gastropods *Patella* spp., *Littorina knysnaensis* (HWN), *Turritella capensis* (quiet water shallower than 3 m), *Oxystele variegata, Burnupena papyracea, Nassarius kraussianus* (mud-banks and weed-beds of estuaries); the bivalves *Loripes liratula* (muddy sand at low tide), *Solen capensis* (muddy sand of estuaries), *Venus verrucosa, Choromytilus meridionalis, Perna perna, Aulacomya ater, Tellina madagascariensis* (extensive infratidally), *Dosinia lupinus, Donax serra* and *Panopea glycymeris.*

None of the constituents of the open-coast or estuarine-lagoonal facies required water depths greater than about 25 m. Modern bathymetric ranges for the species suggests maximum Late Pleistocene water depths at these sites of the order of 0–5 m. This is consistent with the geomorphic evidence.

TEMPERATURE

Since the primary purpose of this paper is a discussion of a southerly migration of tropical and subtropical mollusc species in the last interglacial, the most important criteria are those indicative of temperature. Sea surface temperature inferences may be made by comparing geographic ranges of living molluscan species with those of their fossil counterparts. Although the fossil fauna of the west coast is distinctly modern in character, the estuarine-lagoonal facies assemblages regularly contain several species whose present-day distribution is restricted to tropical and subtropical waters. The modern geographic range end-points of the thermophilic species that live further north on the west African coast are separated by 2 000 km from the fossil occurrences in the south-western Cape, so that the fossil assemblages contain species that do not today live in association. Northward migration of the extralimital species was probably induced by deteriorating environmental conditions. Since the geographic ranges of recent molluscs seem to be determined mainly by temperature (Valentine 1955), it would appear that falling temperature was the compelling factor. It could also be argued that lower temperatures accompanied the advance of the Weischelian ice-sheets, in which case falling sea level would have drained the Late Pleistocene estuaries and lagoons. But with reflooding of these environments in Recent time, the thermophilic molluscs did not return.

Mollusc assemblages in the estuarine-lagoonal facies of the west and south coasts contain a total of more than 20 species that do not sustain populations in those areas today. West coast sites contain 15 such species,

TABLE 2

Present-day Geographic Ranges, Temperature Minima, and Distribution of some Fossil Molluscs

			Fossil Assemblages		
			W. Coast		S. Coast
	WARM WATER TAXA	Minimum Temp. °C*	Open	Estuaries, Lagoons	Knysna
GASTROPODA					
(?)Cantharidus suarezensis	Durban—Tanzania (Kilburn & Tankard, in press)	19			×
Alvania alfredensis	Still Bay—Port Alfred (Kensley 1973)	14		×	
Cerithium kochi	Algoa Bay—Mozambique (Kensley 1973)	16			×
(?)Cerithium scabridum	Red Sea—Quirimba Is. (23,4°S; 40,7°E) (Kilburn & Tankard, in press)	24			×
Cypraea algoensis	Algoa Bay—Natal (Kensley 1973)	16	×		
Marginella piperata	Jeffreys Bay—Zululand (Kensley 1973)	14	×		
Atys cylindrica	Mozambique (Kensley 1973)	21			×
BIVALVIA					
Nuculana bicuspidata	Mauritania—Angola (Nicklès 1950)	17		×	
Ostrea atherstonei	Saldanha Bay—Bushmans River (Korringa 1956)	14		×	
O. stentina	Morocco—Congo Republic (Nicklès 1950)	17		×	
O. algoensis	False Bay—Delagoa Bay (Korringa 1956)	14		×	×
Loripes liratula	Mauritania—Angola (Kilburn & Tankard, in press)	17		×	×
Felania diaphana	Mauritania—Angola (Kilburn & Tankard, in press)	17			×
F. subradiata	Still Bay—Durban (Barnard 1964)	14		×	
Mactra ovalina	Durban—Delagoa Bay (Kilburn 1971*a*)	19		×	×
Scissodesma spengleri	False Bay (Barnard 1964)	14	×		
Tellina ponsonbyi	Still Bay—Zululand (Boss 1969)	14		×	
T. madagascariensis	Gabon—Baia dos Tigres (17°S) (Boss 1969)	17		×	×
Macoma tricostata	Angola (Kilburn & Tankard, in press)	17		×	
Gastrana matadoa	Mauritania—Ivory Coast (Nicklès 1950) Still Bay—Delagoa Bay (Barnard 1964, as *G. abildgaardiana*)	14		×	×
Leporimetis hanleyi	Luanda (Kilburn & Tankard, in press)	17		×	×
Theora alfredensis	Algoa Bay—Zululand (Barnard 1964)	16		×	×
Venerupis dura	Morocco—Angola (Nicklès 1950)	17		×	×
Panopea glycymeris	Mediterranean—Senegal (Kensley 1974)	20		×	

TABLE 2 (*contd.*)

Present-day Geographic Ranges, Temperature Minima, and Distribution of some Fossil Molluscs

				Fossil Assemblages		
				W. Coast		*S. Coast*
COLD WATER TAXA			*Minimum Temp. °C**	*Open*	*Estuaries, Lagoons*	*Knysna*
			Temp. range			
GASTROPODA						
Thais cingulata	Port Nolloth—False Bay	(Kensley 1973)	14–17	×	×	
Burnupena papyracea papyracea	Paternoster—Hermanus	(Kensley 1973)	14–17	×	×	
Nassarius plicatellus	Walvis Bay—Table Bay	(Kensley 1973)	14–17		×	
N. scopularcus	Saldanha	(Kensley 1973)	14–17	×	×	
Conus scitulus algoensis	Table Bay—Kommetjie	(Kilburn 1971*b*)	13–17	×		
BIVALVIA						
Tellimya trigona	Lüderitz—Langebaan Lagoon	(Barnard 1964)	12–16		×	
Lutraria lutraria	Lüderitz—False Bay	(Barnard 1964)	12–15	×	×	

* References: Naval Oceanographic Office, Washington: Spec. Publ. SP-99
Sverdrup *et al.* 1942
Department Transport, Maritime Weather Office, Youngsfield, Cape Town: Sea Surface Temp. Charts

mainly bivalves. These extralimital molluscs, their present-day geographic ranges, and minimum temperature tolerances are shown in Table 2.

It is often difficult to assess the minimum temperature tolerance of living molluscs. Zinsmeister (1974) divides the normal biogeographic range of a taxon into a spawning range, and a non-spawning range. The modern geographic range of *Ostrea atherstonei*, from Saldanha to Bushmans River, implies a minimum temperature tolerance of about 13°C. But it appears that present temperatures in Saldanha Bay are too low for spawning (Korringa 1956). Spawning experiments in this area have confirmed this, and suggest that the oyster larvae may actually originate in an area of higher water temperature. It is possible that several species of molluscs extend their geographic range end-points by inhabiting local pockets of warm water such as estuaries. If this is the case then the temperature minima shown in Table 2 may actually be too low. It is not always clear from the literature whether the range end-points are open-coast, estuaries or embayments. Other difficulties arise from taxonomic problems. For instance, *Macoma ordinaria* and *M. crawfordi* may be geographic variants of the Mediterranean *M. cumana*.

1. *West coast estuarine-lagoonal facies*

Because of physiographic changes at Verlorevlei and the lower reaches of the Berg River, present temperature ranges would be meaningless standards against which to measure Late Pleistocene changes. The present shoreline of Langebaan Lagoon has changed little since the last interglacial, and present temperatures at Churchhaven could be used as an approximation for the other sites as well. Day (1959) gives a surface temperature range for Churchhaven of 13,5°C to 37°C (HW) and 38,5°C (LW).

The fossil assemblage at Verlorevlei (site 3) is represented by 23 species of molluscs, 6 of which are indicative of warm water. These 6 thermophilic species constitute 42 per cent of the total individuals. The modern geographic range of *Loripes liratula* (26,4 per cent of the fauna) is Mauritania to Angola (Nicklès 1950), where its minimum temperature requirement would be 17–18°C. *Ostrea stentina* (2,7 per cent), *Tellina madagascariensis* (8,1 per cent), *Macoma tricostata* (< 1 per cent), and *Venerupis dura* (< 1 per cent) are also tropical west African species and could not tolerate temperatures below about 17°C. *Gastrana matadoa* (4,1 per cent) extends into water as cool as 14°C. Accepting that stenothermal organisms are more critically limited by minimum temperatures than by maximum temperatures (Durham 1950), it would appear that the minimum temperature in this Late Pleistocene estuary must have been 17–18°C, or at least 3°C warmer than present Churchhaven surface temperatures.

At Kruispad (site 12) 8 of the 31 species prefer warm water, and constitute 47,9 per cent of the total individuals. Of these *Nuculana bicuspidata* (3,2 per cent), *Loripes liratula* (15,4 per cent), and *Leporimetis hanleyi* (1,0 per cent) have a minimum temperature requirement of 17–18°C. A significant constituent of this assemblage is *Panopea glycymeris*. Although it forms less than 1 per cent of the total individuals, it is nevertheless very common (because it is a large animal, about 200 mm, and is always found in life orientation, a shell count in a 1 m quadrat would be unlikely to yield more than one or two specimens). *Panopea glycymeris* lives in areas with a temperature range 20–27°C (Kensley 1974), although it could probably tolerate cooler water. This assemblage is thus indicative of a temperature minimum of about 18°C. At Bloemendal (site 11) *Loripes liratula* and *Leporimetis hanleyi* are common.

Three sites examined along the shore of Langebaan Lagoon yielded a significant proportion of thermophilic molluscs: Geelbek (site 19; 7 species in 26 constituting 46,0 per cent of the fauna), Skrywershoek (site 20; 6 species in 19 constituting 32,9 per cent of the fauna), and Churchhaven (site 21/22; 7 species in 31 constituting 28,1 per cent of the fauna in the lower unit; 7 species in 27 constituting 35,5 per cent of the fauna in the upper unit). The dominant thermophilic mollusc content at these sites is as follows:

	Geelbek	*Skrywershoek*	*Churchhaven*	
			Lower	*Upper*
	%	%	%	%
Ostrea atherstonei	5,1	7,1	1,0	5,0
Loripes liratula	20,4	14,1	1,0	4,1
Mactra ovalina	1,0	1,2	2,3	1,7
Tellina madagascariensis	10,2	9,4	23,4	3,3
Leporimetis hanleyi	—	< 1,0	—	—
Venerupis dura	4,1	1,2	—	—

All of these species, except *Ostrea atherstonei* and *Mactra ovalina*, have a minimum temperature requirement of 17°C. *Ostrea atherstonei* is found living today in Saldanha Bay, but temperatures are apparently too low for spawning. It is possible that this species has a minimum temperature tolerance of 14°C. The floor of the present lagoon is underlain by about 3 million metric tons of *O. atherstonei* shells, with little detrital sediment, suggesting optimum temperatures for breeding, and hence probably greatly in excess of 14°C. *Mactra ovalina* has a minimum requirement of 19°C. A minimum temperature in the Late Pleistocene lagoon of about 18°C is indicated, about 4–5°C warmer than the present surface temperature minimum at Churchhaven.

2. *South coast estuarine—lagoonal facies*

A Late Pleistocene site at Knysna was the only one on the south coast examined in detail. But examination of material in collections of the South African Museum shows that very similar fossil faunas exist at Sedgefield, and Groot Brak and Klein Brak estuaries. The fossil assemblage at the Klein Brak estuary contains *Panopea glycymeris*, but their shells are, on average, much smaller than the Kruispad specimens (Kensley 1974).

The Knysna assemblage contains 47 molluscan species, of which 6 are extralimital and which constitute 60,4 per cent of the individuals. But these 6 species include the extinct subspecies *Cantharidus suarezensis fultoni* (9,8 per cent) and *Cerithium scabridum rufonodulosum* (16,3 per cent). Although the geographic ranges of the species is shown in Table 2, it is obviously not certain that the extinct subspecies had the same temperature tolerances. Their Recent relatives *Cantharidus suarezensis suarezensis* and *Cerithium scabridum* have minimum temperature requirements of 19°C and 24°C respectively. *Atys cylindrica* (< 1 per cent) has a minimum temperature requirement of 21°C. Of the bivalves *Felania diaphana* (3 per cent), *Tellina madagascariensis* (< 1 per cent), *Leporimetis hanleyi* (< 1 per cent) and *Venerupis dura* (< 1 per cent) all suggest temperature minima of 17°C. *Loripes liratula* (57,5 per cent) also suggests a temperature minimum of 17°C, but the fact that it occurs in such great numbers, and the fact that all growth stages are present (Fig. 2J), suggest optimum conditions. Together the evidence suggests a temperature minimum in excess of 17°C for the Late Pleistocene estuary. Day *et al.* (1952) gives a temperature range at the railway bridge of 12–24°C.

3. *West coast open-coast facies*

The present-day temperature range on the adjacent open coast is about 13–15°C (Shannon 1966). The fossil assemblage contains only three species which prefer warm water, but which never constitute more than 1 per cent of any assemblage: *Cypraea algoensis*, *Marginella piperata* and *Scissodesma spengleri*. The marked paucity of warm-water species indicates that Late Pleistocene nearshore water temperatures were not very different from the present.

SUMMARY

Before discussing the palaeoclimatic significance of the extralimital molluscan species it may be as well briefly to summarize the evidence.

1. All fossiliferous Late Pleistocene estuarine-lagoonal facies deposits contain extralimital species which usually constitute more than 30 per cent of the individuals of each assemblage, and which indicate minimum water temperatures 4–6°C warmer than the present-day estuaries and lagoons, with minimum temperatures of about 18°C. Kanakoff & Emerson (1959) suggest temperatures in excess of 19°C for similar Californian occurrences.

2. All growth stages of the thermophilic molluscs are present (Fig. 2). The importance of this is that it implies that temperatures were such that the normal spawning range of each mollusc is represented. Normal spawning range is characterized by a population which continually maintains its numbers (Zinsmeister 1974). The large number of individuals and presence of all growth stages show that the thermophilic taxa formed self-sustaining populations that were adequately adapted to the depositional environment.

3. The estuarine-lagoonal facies contain mixed life and indigenous death

assemblages of molluscs. These molluscs obviously lived in environments reflected in the sediments, and have suffered little post-death transportation.

4. The sediments and their mollusc fossils indicate water depths in general less than 5 m.

5. The fact that sediments with high proportions of extralimital molluscan species characterize most Late Pleistocene estuary and lagoonal situations, that these molluscs formed self-sustaining populations and inhabited very shallow water, suggests that the marine transgression to 6 m in the last interglacial was a major event during a climatic optimum.

Zinsmeister (1974) has suggested that similar, well documented occurrences of thermophilic molluscs in Californian Late Pleistocene embayments represent only temporary, non-breeding, members of the community. He believes that periodic local and temporary current changes introduced tropical mollusc larvae into areas of cooler water, and that these molluscs represent only temporary members of the community since temperatures would have been too low for them to maintain self-sustaining populations.

Zinsmeister's arguments stem from the fact that previous studies paid scant attention to the population dynamics, and consequently they fail to prove the presence of self-sustaining populations. Similar occurrences in the south-western Cape support the view that these faunas are the result of a warmer climate which must have affected the whole world. Age-wise these deposits are also similar and probably coincide with a high climatic peak (substage 5e) and sea level up to 7 m higher than present at 120 ka (Shackleton 1969).

6. Configuration of the coastline was probably very important. Today a low Palaeozoic rock bar just above high-tide level keeps the sea out of Verlorevlei. A slight rise of sea level would create radical changes at Verlorevlei. Likewise the lower reaches of the Berg River formed a prominent estuary due to flooding by last interglacial high sea levels. Normally one would expect to find an overlap of geographic ranges of tropical and temperate species. In an overlap area the tropical species would be restricted to inshore, protected environments, and temperate species would live in the cooler open coast sites (Emerson 1956).

PALAEOCLIMATIC INTERPRETATION

REVIEW OF PRESENT CLIMATE AND HYDROLOGY

The south-western Cape has a Mediterranean-type climate. Hot, dry summers are the result of the dominant anticyclones in those months, while depressions associated with westerly winds bring rainfall in winter.

Hart & Currie (1960) have summarized the effect of the wind system on the climate of the south-western Cape Province. A subtropical high-pressure system is centred between 26° and 30°S. To the south this high-pressure system borders on the 'westerlies' causing a steep pressure gradient. The south-easterly winds of the south-western Cape are the result of winds blowing anticyclonically around this high-pressure system. In summer the centre of the anticyclone lies at about 30°S and brings strong south-easterly winds to the south-western regions, but in winter it moves northwards to 26°S. The westerly wind system follows the anticyclone northward and the southern Cape is then frequented by depressions which bring rain from the south-west Atlantic, although the Namib Desert is still influenced by the Trade Wind belt.

The west coast of southern Africa, like the west coasts of other countries in similar latitudes, is characterized by a linear belt of centres of upwelling of cold subsurface water (Central Water) from Lüderitz to the Cape Peninsula (Fig. 1 insert). There is a north–south isotherm lineation with the coldest and least saline water near the coast (Shannon 1966). This upwelling, the Benguela Current, varies in intensity depending upon the wind system and local topography. The upwelling phenomenon arises from the displacement of surface water northwards and off-shore by the south-easterly wind system. Cooler subsurface water wells up to replace this warmer water. The result of this active upwelling is a complex system with tongues of cold water alternating with intrusions of warmer oceanic waters, and all diverging to the north-west (Bang 1971). Bang defines the Benguela Current as the area east of a belt of off-shore divergence within which the oceanic processes are dominated by short-term atmospheric interactions.

During the winter months when the anticyclone centre moves northward, weakening of the southerly wind component results in weakening of the upwelling system also. With less upwelling the surface waters over the inner part of the continental shelf are warmer by 2°C, but off-shore a drop in temperature tends to minimize this affect. With weakening of the Benguela Current system and the greater prominence of westerly and north-westerly winds, a southward-flowing inshore counter-current develops. Shannon (1966) mentions a predominantly southward-flowing counter-current between Lambert's Bay and Cape Point which is present during all seasons, but most marked in winter. A southward-flowing counter-current carries 'seeboontjies' from Angola and driftwood from the Orange River southwards (Wagner & Merensky 1928). Surface temperatures at the Orange mouth rise noticeably when the north-westerly winds blow.

The highest surface-water temperatures are encountered in the lagoons and estuaries which are protected from the effects of upwelling. The temperature range in Langebaan Lagoon, 10–39°C (Day 1959), contrasts markedly with that of the near-by open sea, 13–15°C (Shannon 1966). During the summer months temperatures in Langebaan Lagoon are at a maximum, while those of the open sea drop.

The currents off the east and south coasts, the Mozambique Current and Agulhas Current, have been studied by Clowes (1950), Orren (1963, 1966), and Darbyshire (1964). Both of these currents are southward extensions of the great South Equatorial Current which flows westwards across the Indian Ocean. At 26°S the Mozambique Current is met by the southern branch of the South

Equatorial Current, which is divided by Madagascar, and they combine to form the Agulhas Current. The Agulhas Current is finally deflected by the Agulhas Bank (Clowes 1950) (Fig. 1).

Upwelling does take place off Cape Agulhas but it is a geostrophic upwelling, i.e. the upwelling varies with the velocity of the current. Here the Agulhas Current is weakest and Agulhas water retreats northwards in winter, thus allowing Central Water to reach the surface. In summer, when the Agulhas Current is flowing at its strongest, it overrides the Central Water (Darbyshire 1964). Sometimes in summer the warm Agulhas Current moves away from the south coast and allows cold Central Water to replace it inshore, and within a day or two the temperature may fall by as much as 10°C (Day 1963). Schell (1968) describes the occasional penetration of the Agulhas Current round the Cape Peninsula into the South Atlantic.

LATE PLEISTOCENE CLIMATE

It would be expected that the intensity, and probably position, of the anticyclones would vary with the solar radiation. A climatic optimum at 120 ka produced temperatures warmer than at any other time in the last 120 ka (Shackleton 1969). The anticyclone would have moved south of latitude 30°S (Van Zinderen Bakker 1967: fig. 6). This would lead to the linear west coast upwelling belt moving south in response, and the winter-rainfall area would be more strictly restricted to the south-western Cape. Such a southward movement would be accompanied by more pronounced upwelling off the west coast than at present, and would operate over a longer period of time just as happens on the Namib Desert coast. Since the Central Water originated in the Southern Ocean, and since the Antarctic ice-sheet was essentially stable throughout the Pleistocene (Mercer 1968), it is unlikely that the upwelling water would have been any colder than the present. This is confirmed by the fossil molluscs from the open-coast facies which suggest little temperature change. Addicott & Emerson (1959) and Valentine (1955) have also suggested intensified nearshore upwelling and a poleward expansion of isotherms to explain their mollusc faunas.

Eustatic rise of sea level would have changed the configuration of the coast by forming salt-water estuaries at Verlorevlei and the Berg River, as well as at numerous sites along the south coast. The present coast is not as embayed as the Late Pleistocene coast would have been. Thermally anomalous assemblages existed contemporaneously only in the vicinity of the protected bays where the increased solar radiation of the last interglacial heated the surface water considerably.

Periodic current changes permitted the introduction of tropical mollusc larvae into these pockets of warm water. The intensification of atmospheric circulation that led to more pronounced upwelling presumably also affected the inshore counter-current which possibly flowed more strongly than at present. Isaacs & Sette (1959) described anomalous wind fields in the Pacific area during

1957 and 1958 which so changed the oceanic circulation that tropical taxa were found far north of their expected ranges. This demonstrates that circulation changes as proposed in this paper do happen at present, albeit less frequently and less pronounced than is here suggested.

On the east coast with intensification of the air circulation intensification of the present summer conditions would also be anticipated. Presumably the Agulhas Current flowed more strongly than today and continually overrode the Central Water, perhaps with frequent eddies of Agulhas water around the Cape Peninsula. This would limit the likelihood of sudden incursions of cold water, such as presently affect the Knysna estuary in summer and cause temperatures to drop between 10 and 15°C (Korringa 1956).

These possible changes in the oceanic circulation during the hyperthermal period would have had far-reaching effects on the distribution of molluscs. Because of the low migratory ability of molluscs in the post-larval stage, their geographic distribution depends primarily on the dispersion of larvae. Distribution of the planktonic larvae depends upon ocean currents. About 85 per cent of tropical marine molluscs have a free-swimming pelagic larval stage which can exist, on average, three to four weeks before settling (Zinsmeister 1974). Dietrich (1935 in Korringa 1956) gives the velocity of the Agulhas Current as 50 km per day. At this rate larvae could be transported 1 000 km before metamorphosis. Larvae can apparently withstand sudden changes of temperature; Korringa mentions a change from 25° to 2°C which did not adversely affect oyster larvae.

A general southward movement of isotherms on the west and south coast is envisaged. This would have brought the tropical mollusc zone closer to the south-western Cape. Periodic expansions of the warm-water isotherms coupled with an intensified inshore counter-current on the west coast would have enabled tropical mollusc larvae to pass the cold Benguela barrier. If the larvae reached the sheltered estuaries and lagoons of the south-west coast, increased solar heating (substage 5e) would have allowed these molluscs to sustain their populations and persist there even after the open-coast thermal barrier became impassable again. Those thermophilic larvae that reached metamorphosis on the open coast may well have survived, but there is no evidence that they were able to sustain their populations. South coast estuarine facies show that larvae from the tropical west African coast were able to pass the Cape Peninsula: e.g. *Tellina madagascariensis*, *Loripes liratula*, *Leporimetis hanleyi*, *Venerupis dura*, *Panopea glycymeris*. The Agulhas Current was also able to transport Indo-Pacific mollusc larvae around the Peninsula to the west coast sites. In these sheltered embayments warm-water taxa survived as relicts.

DISCUSSION

The occurrence of thermophilic molluscs in Late Pleistocene sediments of the south-western Cape far beyond their present-day geographic range end-points is not unique. Similar occurrences in California have been extensively studied, and the same conditions appear to have operated in the Miocene where the configuration of the coastline was very different from the present. The San Joaquin basin was a protected embayment in the Late Miocene, and there relict faunas persisted long after the temperate faunas had spread southward along the open coast (Addicott & Vedder 1963). The thermally anomalous Late Pleistocene molluscs also lived in shallow protected embayments (Addicott & Emerson 1959). The only significant point of difference between the two regions is that the open-coast facies of the Cape coast contains molluscs which nearly all live on the adjacent coast, while the Californian open-coast facies contains a fauna that reflects cooler water than the present. Valentine (1955) proposed that during the last interglacial of California upwelling was intensified, while at the same time the warmer water of the sheltered embayments was derived from increased solar radiation. He also suggested a general warming of the oceanic waters by increased solar heating.

The Late Pleistocene estuarine-lagoonal facies of the Cape Province are attributed to a eustatic rise of sea level which changed the configuration of the coast and produced a great number of estuaries where the effects of seasonal upwelling were excluded. A southward movement of the south Atlantic anticyclone at this time shortened the cold-water barrier on the western open coast by causing a southward shift of the Benguela Current, and possibly strengthened the inshore counter-current, so that thermophilic mollusc larvae were able to migrate southwards where they could sustain their populations in the solar-heated estuaries and lagoons. It would appear that the present temperatures are too low for breeding.

This history contrasts with that of the Early Pleistocene when sea temperatures on the open coast were much warmer than at present. The last of these warm-water open-coast episodes is associated with the 45–50 m transgression complex of the Namaqualand coast (Carrington & Kensley 1969). *Striostrea margaritacea* was common on the open coast, forming the so-called 'oyster line' (Haughton 1931). This oyster requires a minimum water temperature of 25°C in summer (Korringa 1956). The 45–50 m transgression complex sediments were probably pre-glacial Pleistocene. Such warm conditions must have been in response to the warmer conditions prevailing in the northern hemisphere, since the Antarctic ice-sheet is thought to have been stable throughout the Pleistocene (Mercer 1968). Warming of the northern hemisphere would have moved the intertropical convergence farther south than even its Late Pleistocene position. This would have moved the South Atlantic anticyclone south, and with it the belt of upwelling, bringing tropical waters down the Namaqualand coast. But *Striostrea margaritacea* is totally absent from Early Pleistocene deposits in the Saldanha area, suggesting that cool water, and upwelling, were still dominant there.

If the model for a southward shift of the anticyclonic system in the last interglacial is correct, then one would expect the opposite trend during the Weischelian. Lamb (1961) suggests that Ice Age circulation was marked by intensified circulation of the belt of westerlies, and greater mobility in the subtropical anticyclones, which generates upwelling systems such as the Benguela Current. Van Zinderen Bakker (1967, in press) presents evidence to show that during hypothermal periods the influence of the anticyclones and the Benguela Current would have shifted northwards to the equatorial regions. Displacement of the westerlies towards lower latitudes would have expanded the winter-rainfall area of the southern Cape, and would have caused a northerly shift of the Namib Desert. Tankard & Schweitzer (1974) have demonstrated, from Die Kelders cave sediments, that wetter conditions in the Weischelian coincided with a cooler period. Butzer (1973) has found a similar record in the Nelson Bay cave. A northward migration of the belt of westerlies would have resulted in a longer rainy season, if not year-round precipitation.

Finally, this study suggests a possible correlation of the last interglacial deposits of the Cape Province with the Eutyrrhenian of the Mediterranean. Although warping of the Eutyrrhenian shorelines is universal (Richards 1962), Bonifay & Mars (1959) have attempted to restore these shorelines to their original elevations. They attribute the Eutyrrhenian shoreline to a transgression to 2–3 m a.s.l. Chronologically the Eutyrrhenian shoreline and last interglacial shorelines of the south-western Cape appear to be similar.

The *Strombus* fauna of the Eutyrrhenian deposits is characterized by *Strombus bubonius* and other species typical of Senegal and west Africa (Richards 1962) which suggest warmer hydroclimates than today. Like the warm water fauna of the south-western Cape, the *Strombus* fauna can also be attributed to poleward expansion of isotherms, and once in the Mediterranean the molluscs remained a relict fauna which survived in water heated by increased solar radiation.

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Family Nuculanidae

Nuculana (*Lembulus*) *bicuspidata* (Gould, 1845)

Figs 14–15A

Nucula (*Leda*) *bicuspidata* Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (figs 8a–b).
Nucula largillierti Philippi, 1861: 87
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

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ANTHONY J. TANKARD

THERMALLY ANOMALOUS LATE PLEISTOCENE MOLLUSCS FROM THE SOUTH-WESTERN CAPE PROVINCE, SOUTH AFRICA

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By

BRIAN KENSLEY

Cape Town Kaapstad

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By

Brian Kensley

South African Museum, Cape Town

(With 5 figures)

[*MS. accepted 17 June 1975*]

ABSTRACT

A new species of *Callianassa* is described from Port Alfred, South Africa. Three species from Mauritius, viz. *C. mauritiana*, *C. armata*, and *C. indica* are figured and earlier descriptions are supplemented. The latter two species are new records for Mauritius. *C. kraussi* is recorded as a Pleistocene fossil from Table Bay and Port Elizabeth.

CONTENTS

	PAGE
Introduction	47
Systematic account	48
Acknowledgements	57
References	57

INTRODUCTION

When two specimens of a large *Callianassa* from the Kowie River at Port Alfred were submitted to the South African Museum for identification, it was found that they belonged to none of the six species previously recorded from South Africa (Kensley 1974). Use of Barnard's key (1950: 505) ran the species down to *C. martensi* Miers. In an attempt to solve this problem of identification, two species of mud-prawn were obtained on loan from the Mauritius Institute, a few specimens were collected in Mauritius by D. Hatton and given to the South African Museum, and the type specimens of the two species of *Callianassa* previously recorded from Mauritius were obtained on loan from the British Museum.

As a result, the specimens from the Kowie River were found to be undescribed. The specimens from Mauritius were found to be new records for the island, and it was thought useful to figure them and to supply brief descriptions. Also, it was thought desirable to supplement the description of *Callianassa mauritiana*. The other species from Mauritius, viz. *C. martensi* Miers, has recently been very thoroughly redescribed (Tirmizi 1974).

In the accompanying figures, all dimensions are in millimetres.

Ann. S. Afr. Mus. **69** (3), 1976: 47–58, 5 figs.

SYSTEMATIC ACCOUNT

Callianassa armata A. M. Edwards

Fig. 1A–H

Callianassa armata A. M. Edwards, 1870: 90, pl. 1. De Man, 1902: 754; 1928*a*: 109.

Description

♂ Carapace with spinose acutely triangular rostrum reaching to distal end of cornea; well-defined antero-lateral spine present.

Eyestalks reaching to end of basal peduncular segment of antennule, distally slightly curved away from midline; cornea situated dorso-laterally at about midpoint of outer eyestalk margin; outer proximal part of eyestalk bearing three or four tiny spinules.

Antennular peduncle three-segmented, second segment about half length of third. Two distal antennal peduncular segments slender, subequal, basal segment bearing distal spine.

Third maxilliped with propodus, carpus, merus, and ischium moderately expanded; propodus with notch on antero-distal margin; ischium bearing on inner surface a marked distal crest armed with about twelve teeth of varying sizes, proximal portion bearing three separated spines.

Larger cheliped with dactylus strongly curved, cutting edge uneven, with no well-marked teeth or tubercles; propodus with upper margin bearing three strong spines; cutting edge of thumb with single blunt proximal tubercle, ventral margin proximally slightly dentate; carpus shorter than propodal palm, ventral margin bearing nine spines; merus with two spines on dorsal margin, seven on ventral margin; ischium armed with row of ten spines, increasing in size distally.

Finger and thumb of smaller chela gaping, cutting edge of finger unarmed, that of thumb with blunt tubercle at about midpoint; upper margin of palm bearing three spines; carpus armed with four spines on ventral margin; merus bearing three spines on dorsal margin, four on ventral margin; ischium with row of fourteen spines, distal four longer than more proximal spines.

Propodus of third pereiopod with posterior lobe not very marked, evenly rounded. Telson broader than long, with semicircular seta-bearing ridge in proximal third, and two very faint radiating rounded ridges not quite reaching distal margin.

Uropodal exopod markedly bipartite, anterior portion about half length of posterior, two portions separated by a curved ridge bearing a sharp spine proximally; endopod lanceolate with rounded tubercle at base.

Material

1 ♂, Mauritius Institute 956. Carapace length (including rostrum) 28,4 mm. Total length 98 mm.

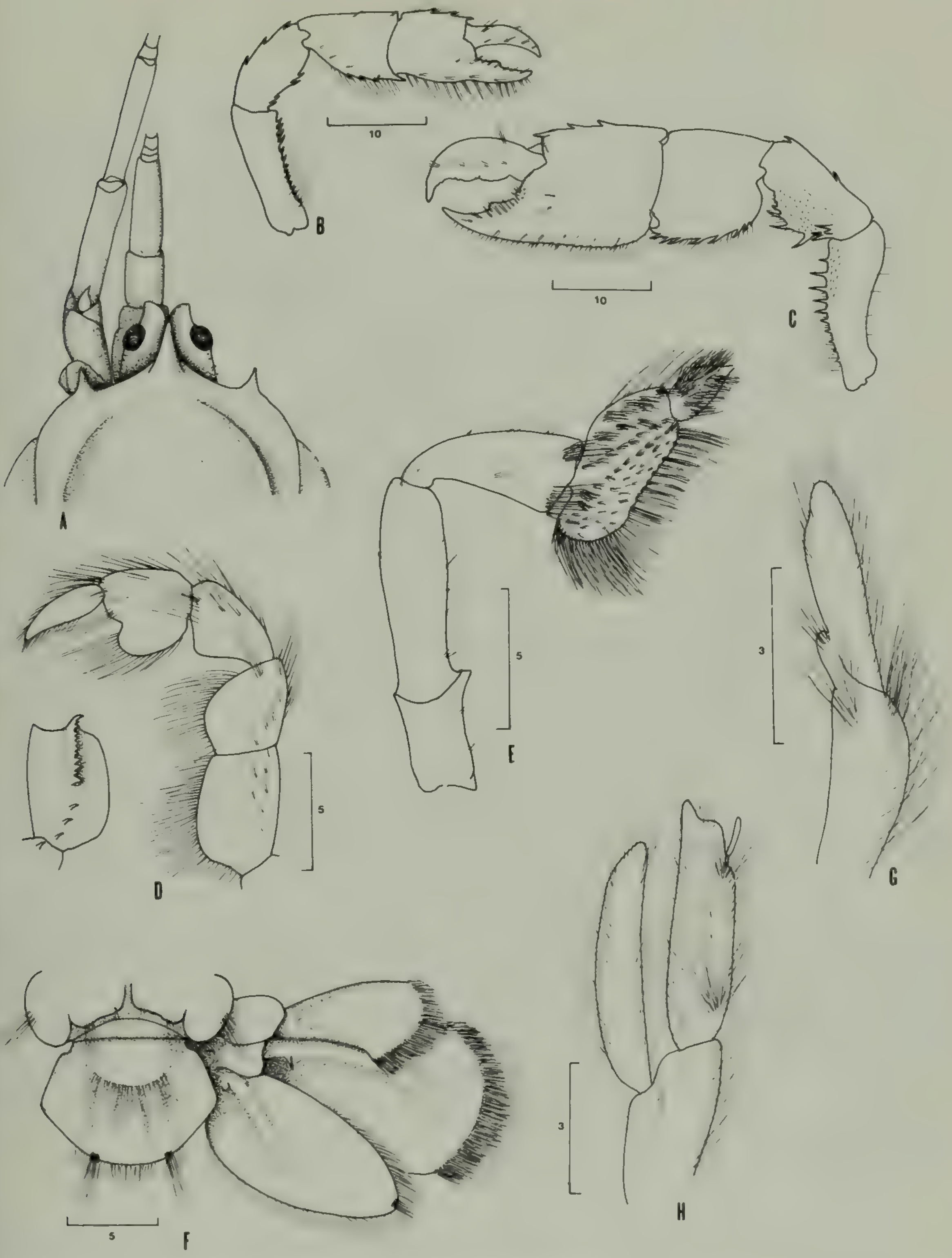

Fig. 1. *Callianassa armata* ♂

A. Anterior carapace, eyestalks, and antennae in dorsal view. B. Smaller cheliped. C. Larger cheliped. D. Third maxilliped, with inner view of ischium. E. Third pereiopod. F. Telson and uropod. G. First pleopod. H. Second pleopod.

Previous Records

Fiji Islands; Ternate, India.

Remarks

Callianassa armata was described from a female of 125 mm from the Fiji Islands, while the second specimen was a juvenile female from Ternate, India. The present specimen, being a male, may account for a few discrepancies with the original description. For example, De Man (1928*a*) in his key to the species of the subgenus *Callichirus* described the uropodal exopod as lacking a spine—this spine is obviously present in the male. In the latter, the sixth pleonal segment is two and a half times the length of the telson, while in the Fijian female this segment is three times the length of the telson.

Callianassa indica de Man

Fig. 2A–E

Callianassa indica de Man, 1905: 605; 1928*a*:100, 160, pl. 17 (fig. 26).

Description

♀ Rostrum very short, obtusely triangular, antero-lateral angles rounded, bearing tufts of setae.

Cornea dorso-lateral; eyestalks with rounded apex armed with three or four very small blunt tubercles.

Propodus of third maxilliped as long as broad, inner face of ischium bearing curved row of spines, those of distal part of row closely packed, unequal, longer spines alternating with three or four short spines, more proximal spines separate and subequal.

Larger cheliped with dactylus strongly curved, cutting edge bearing two strong tubercles at about midpoint, thumb of propodus proximally finely denticulate; palm of propodus one and a half times longer than dactylus, ventral margin bearing about nine small serrations; ventral margin of carpus evenly convex; ventral margin of merus armed with ten small teeth; ventral margin of ischium bearing about twelve small teeth, increasing in size distally.

Smaller cheliped with finger and thumb gaping, equal in length to palm of propodus; carpus and merus subequal in length, unarmed.

Material

1 ♀. Mauritius Institute 948, Black River, Mauritius. Carapace length (including rostrum) 22,5 mm. Total length 84 mm.

Previous Records

Kangeang Reef, Bay of Kankamaraän, East Indies.

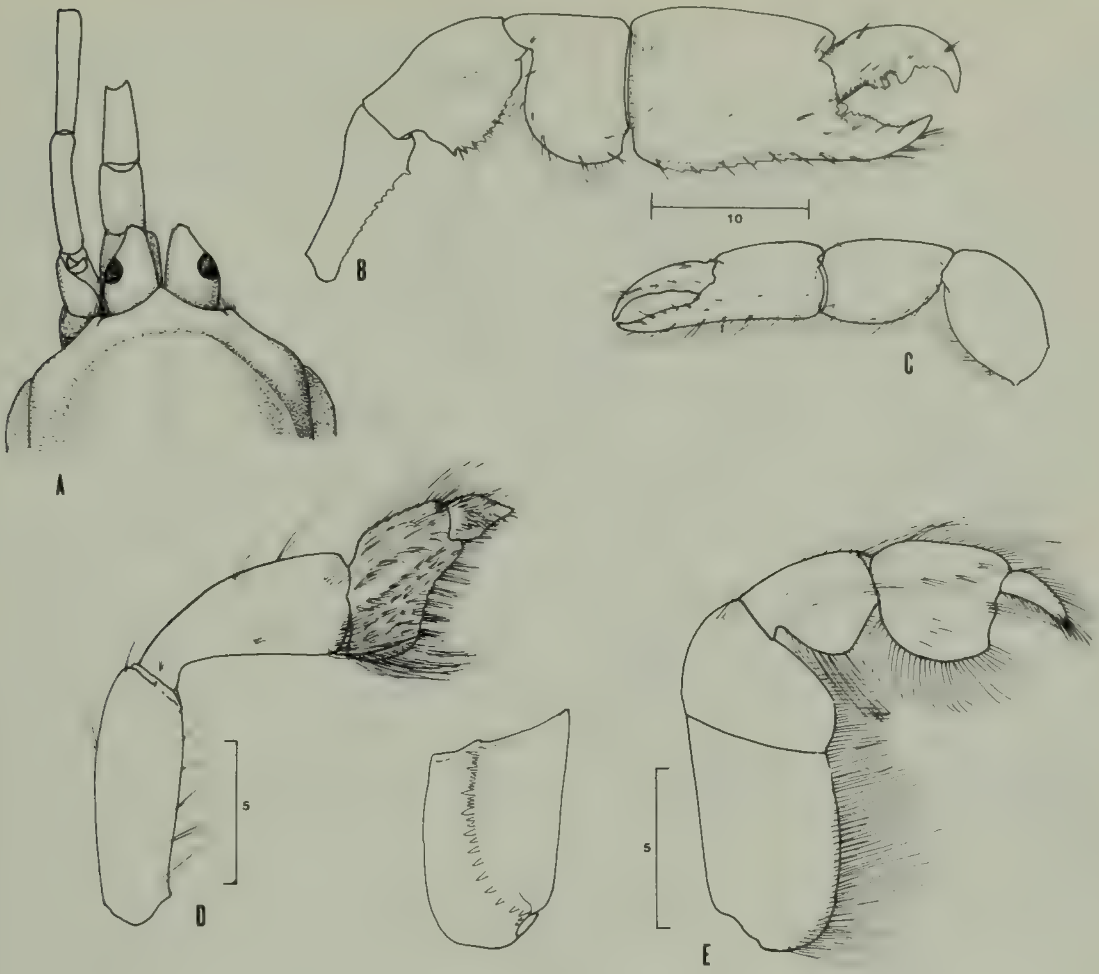

Fig. 2. *Callianassa indica* ♀

A. Anterior carapace, eyestalks, and antennae in dorsal view. B. Larger cheliped. C. Smaller cheliped. D. Third pereiopod. E. Third maxilliped, with inner view of ischium.

Remarks

This is the second record of a species that was described from a single male, total length 90 mm, which lacked the larger cheliped. The above figures and description, although of a mature female, supplement De Man's description.

Callianassa mauritiana Miers

Fig. 3A–H

Callianassa mauritiana Miers, 1882: 341; 1884: 15, pl. 1 (fig. 2). Nobili, 1906: 106, figs 5, 6. De Man, 1928*a*: 99; 1928*b*: 10, pl. 2 (fig. 4). Michel, 1974: 256.

Description

In spite of the descriptions given by Miers, Nobili, and De Man, it was felt that additional figures of this rarely recorded species would be useful. The figures were done from the male and female syntypes from the British Museum (Natural History) collection.

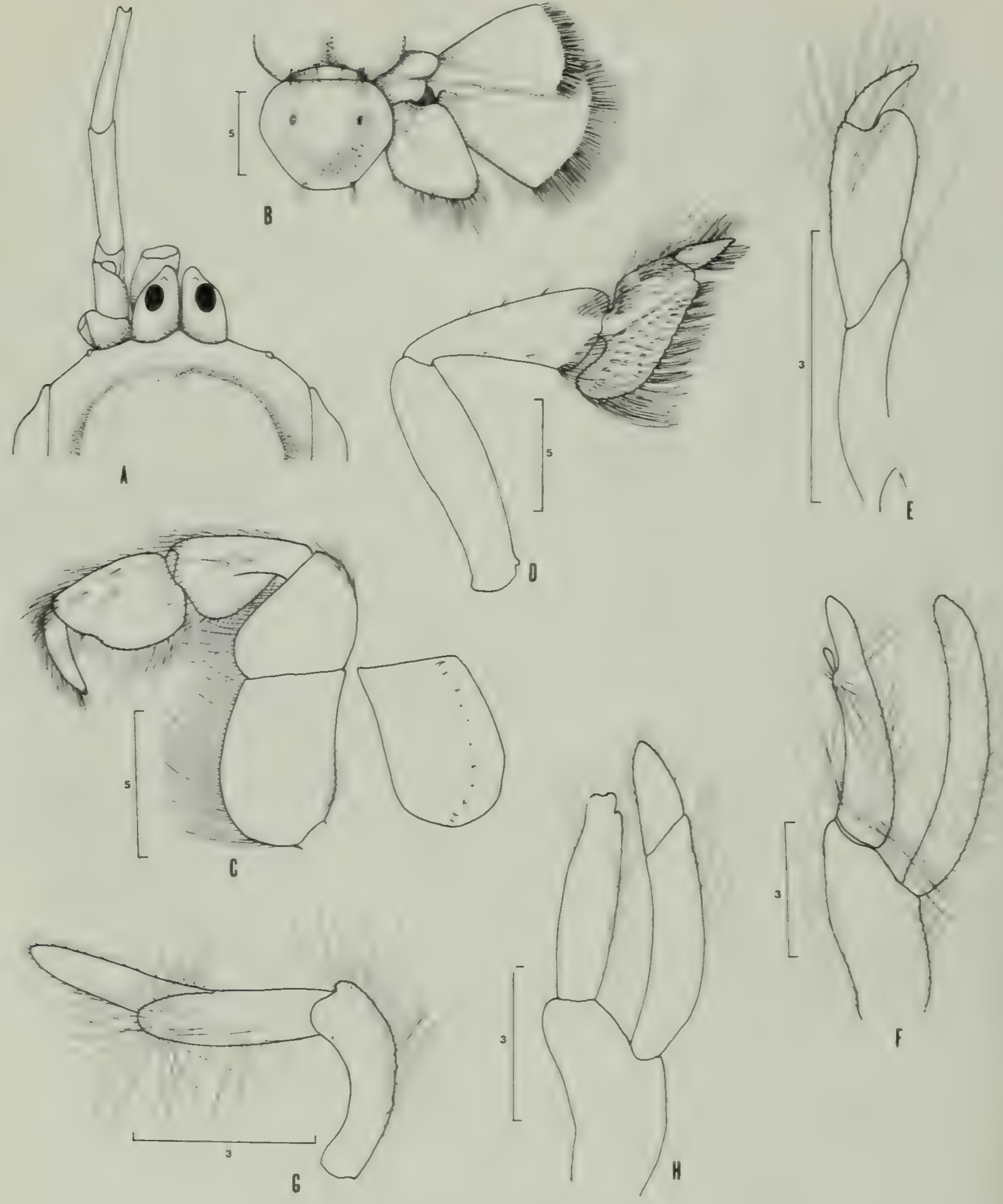

Fig. 3. *Callianassa mauritiana*

A. Anterior carapace, eystalks, and antennae in dorsal view. B. Telson and uropod. C. Third maxilliped, with inner view of ischium. D. Third pereiopod. E. First pleopod ♂. F. Second pleopod ♂. G. First pleopod ♀. H. Second pleopod ♀.

Eyestalk with cornea situated dorsally, slightly distal to midpoint, with tiny but distinct rounded tubercle distal to cornea.

Third pereiopod with propodus having a curved posterior lobe.

Uropodal exopod bipartite, anterior portion only slightly shorter than posterior, with spine at base. This spine only developed in adult.

Material

Mauritius, SAM–A13636	♂	carapace length	12,0 mm	total length	—
	♀		11,3 mm		43 mm
	♀		9,0 mm		31 mm

Previous Records

Mauritius; Red Sea.

Remarks

Miers (1882: 341) expressed the opinion that the detached large chela in the container with the two syntypes probably did not belong to either of the specimens, but to a distinct and larger individual. This need not necessarily be so, as the species seems to be characterized by a disproportionally massive larger cheliped. In an immature male with a carapace length of 12,0 mm the larger cheliped has a length of 40 mm.

Callianassa pixii sp. n.

Fig. 4A–H, 5A–K

Description

♀ Carapace with oval shield well defined; rostrum short, acute, triangular, with median keel running on to carapace; front tridentate, lateral teeth only slightly shorter than rostrum, also slightly keeled. Eyestalks contiguous for whole length, tapering from about mid-length to acute apex; cornea situated dorsally in distal half, hardly visible. Eyestalks reaching to end of first antennular peduncle segment.

Third peduncular segment of antennule slightly more than twice length of second. Antennal peduncle not quite reaching distal end of antennular peduncle, two distal segments subequal.

Mandibular palp three-segmented, distal segment set with numerous setae, equal in length to two proximal segments together; incisor portion weakly chitinized, with about thirteen small teeth on cutting edge; molar portion a blunt flattened structure set with plumose setae.

First maxilla, palp slender, distal portion flexed, median edges of lobes densely fringed with setae.

Second maxilla also densely fringed with setae.

Epipod of first maxilliped with posterior portion longer and broader than anterior part.

Second maxilliped pediform, exopod slender, leaf-like, endopod with apical segment bearing cluster of short, stiff setae, rest of appendage fringed with long setae.

Third maxilliped pediform, lacking exopod, three distal segments together slightly shorter than two proximal segments; merus and ischium fringed with long setae, together four and a half times longer than wide; inner face bearing another fringe of setae; propodus and carpus each with dense bristle pad on inner face.

First pereiopods subequal, finger and thumb slightly shorter than palm of propodus, dactylus curved only at tip, cutting edge entire, thumb of propodus

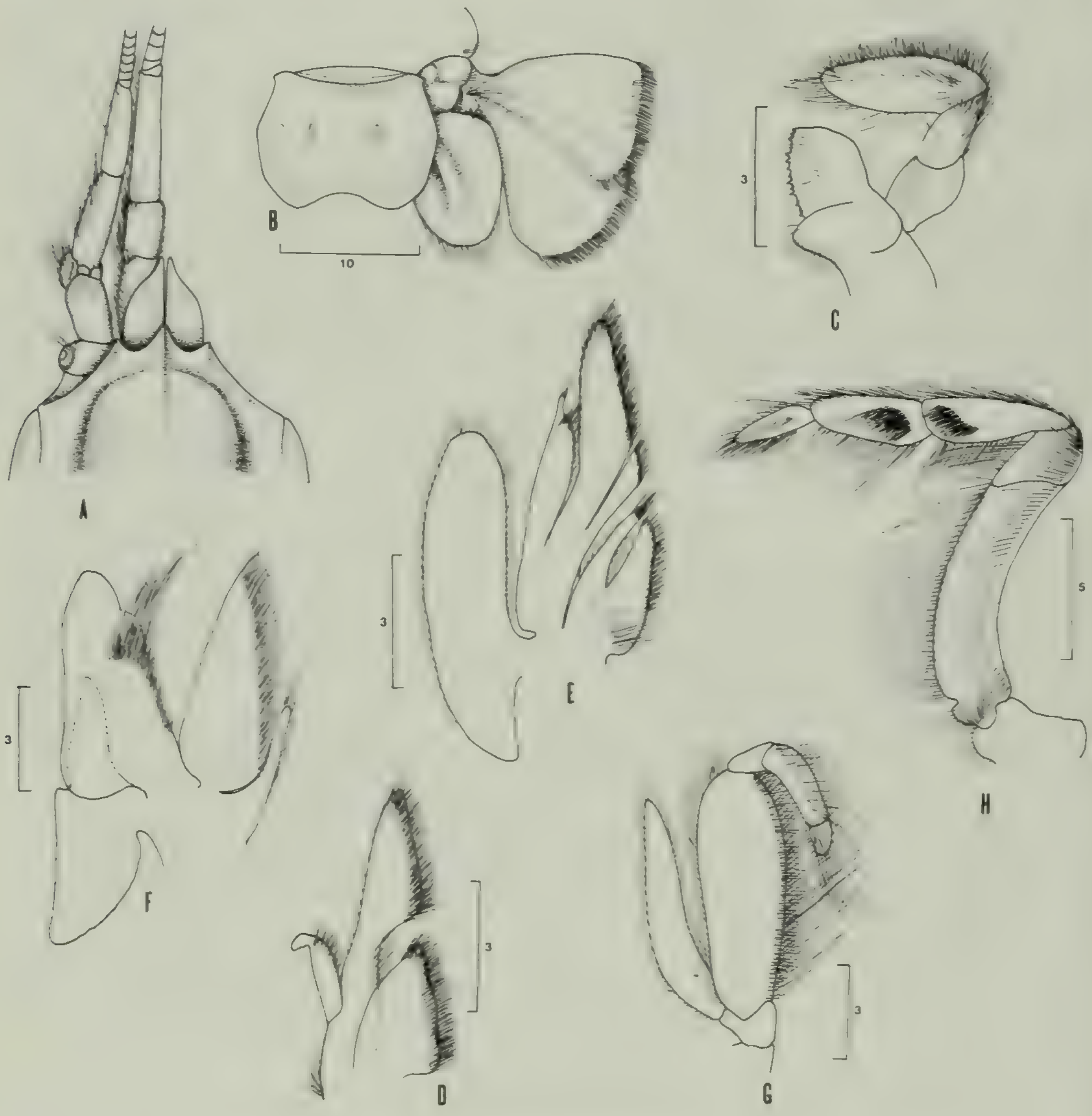

Fig. 4. *Callianassa pixii* sp. n.

A. Anterior carapace, eyestalks, and antennae in dorsal view. B. Telson and uropod. C. Mandible. D. First maxilla. E. Second maxilla. F. First maxilliped. G. Second maxilliped. H. Third maxilliped, inner view.

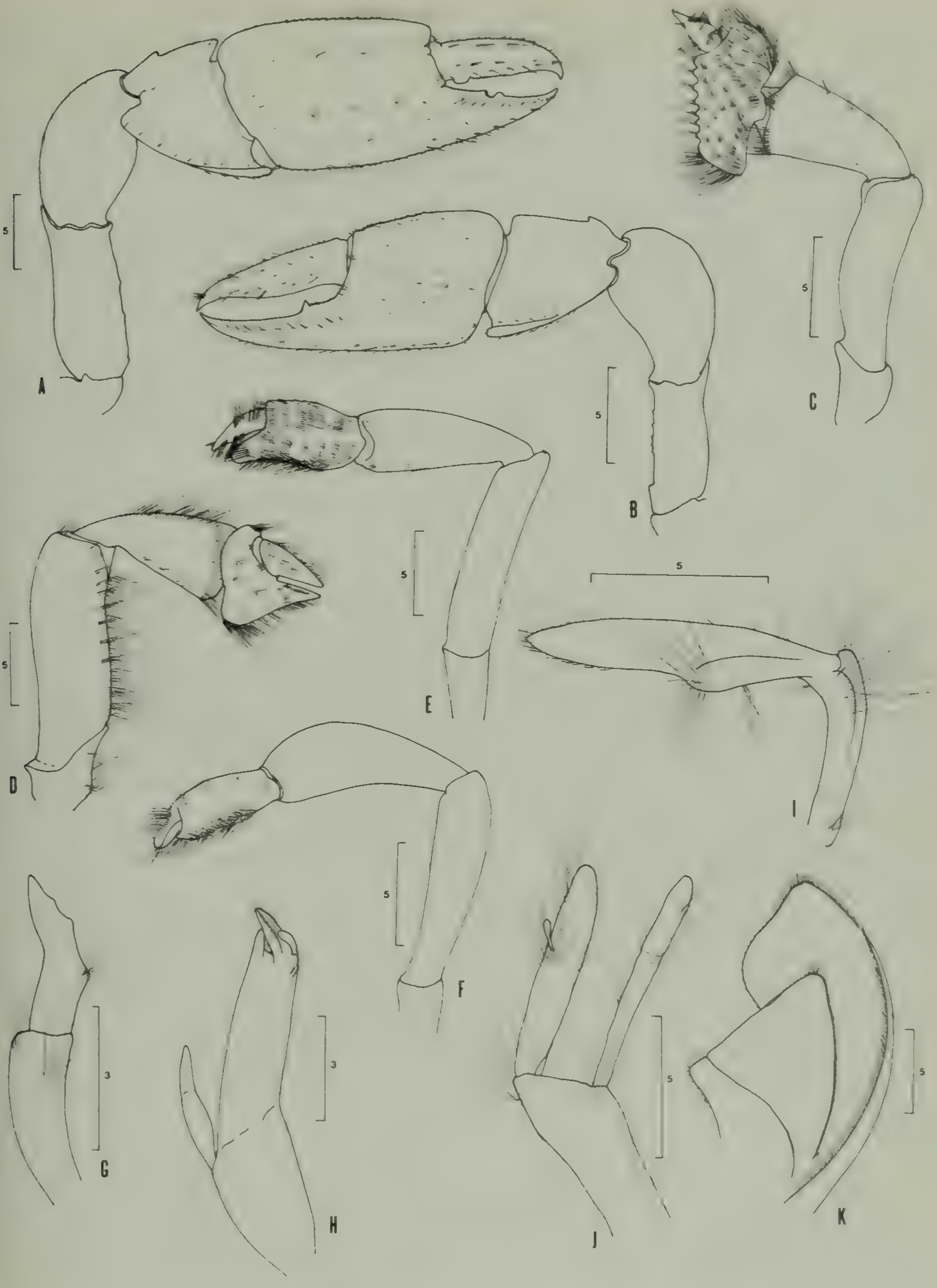

Fig. 5. *Callianassa pixii* sp. n.

A. Larger cheliped ♂. B. Smaller cheliped ♂. C. Third pereiopod. D. Second pereiopod. E. Fourth pereiopod. F. Fifth pereiopod. G. First pleopod ♂. H. Second pleopod ♂. I. First pleopod ♀. J. Second pleopod ♀. K. Third pleopod ♂.

with large triangular tooth at midpoint of cutting edge, followed proximally by fine denticulations; carpus about half length of palm of propodus, upper margin entire; merus longer than carpus; ischium with about six tiny denticulations on lower margin.

Second pereiopod chelate, with dactylus, propodus, and carpus together subequal to merus in length, cutting margins of dactylus and propodus straight, all segments bearing numerous elongate setae.

Third pereiopod with posterior lobe of propodus oblique-truncate.

Fourth pereiopod with propodus having distal thumb-like lobe slightly shorter than dactylus, and therefore incompletely chelate; dactylus and propodus set with numerous short stiff setae.

Fifth pereiopod chelate, dactylus and propodal thumb apically spooned, set with patches of short dense setae.

First pleopod uniramous, longer distal portion flexed at right angle to basal portion, bearing clumps of elongate setae.

Second pleopod biramous, rami subequal in length, inner ramus bearing small lobe on distal half.

Telson broader than long, distal margin concave.

Uropodal exopod bipartite, anterior portion only slightly shorter than posterior, with spine at base, both portions fringed with short setae; endopod oval, shorter than exopod, with rounded longitudinal ridge.

♂ Larger cheliped subequal in length to smaller cheliped, but propodus and carpus broader; finger and thumb shorter than palm of propodus; dactylus only distally hooked, with blunt tubercle near base of cutting edge; thumb of propodus with slight notch and fine denticulations proximal to blunt tubercle at about midpoint of cutting edge; upper margin of palm finely denticulate; carpus with single tooth on upper margin; lower margin of ischium with two or three barely discernible teeth.

Smaller cheliped similar to first pereiopods of female, but possessing single tooth on upper margin of carpus.

First pleopod about half length of second pleopod, uniramous, two-segmented, distal segment with three slight tuberculations.

Second pleopod biramous, outer ramus half length of inner, latter with trilobed apex, middle lobe largest.

Material

Holotype ♀ SAM–A13637 carapace length 27,0 mm total length 85 mm.

Allotype ♂ SAM–A13637 carapace length 26,0 mm (posterior pleon and telson missing). Kowie River estuary, Cape Province, South Africa.

Remarks

Callianassa pixii belongs to that group of species of the subgenus *Callichirus* which is characterized by the possession of a pediform third maxilliped. Of this group, *C. pixii* most closely resembles *C. guineensis* de

Man, described from the Gold Coast (De Man 1928*b*). Several differences make the separation of these two species quite simple.

Although the third maxillipeds are very similar, in *Callianassa pixii* the merus and ischium have a more definite curvature than in the west African species. In the latter, the antennae are distinctly shorter and more slender than the antennules, eyestalks are not contiguous, and the cornea of the eyes are large and distinct. In *C. pixii* the antennae are only slightly shorter than the antennules and of similar thickness. The eyestalks are contiguous and the cornea small and hardly defined. The telson and uropodal endopods of the two species are similar, but the uropodal exopod in *C. guineensis* is unevenly bipartite, while in the Kowie species the two portions of the exopod are of similar length and breadth. De Man's specimen of *C. guineensis* was a juvenile, thus a comparison of the cheliped structure is of little value.

The species is named for Mr Pixie John, well-known local figure of Port Alfred.

Callianassa kraussi Stebbing

Callianassa kraussi Barnard, 1950: 506. Kensley, 1974: 277.

Remarks

Numerous dactyli and propodi of the larger chelipeds of this species have been collected from Pleistocene raised beaches at Swartkops, near Port Elizabeth, and at Milnerton, Table Bay. Several are larger and more robust than those of the largest known living specimens of the species.

ACKNOWLEDGEMENTS

My sincere thanks are due to the following for making material available for study: Dr R. W. Ingle, of the British Museum (Natural History) for the loan of type material of *Callianassa martensi* and *C. mauritiana*; Dr C. Miche of the Mauritius Institute, for the loan of specimens of *C. armata* and *C. indica*; Dr A. T. Forbes for donating the specimens of *C. pixii* to the South African Museum, and for useful information; and Mr D. Hatton, for the donation of specimens of *C. mauritiana* to the South African Museum.

I am grateful to Professor Nasima Tirmizi of the University of Karachi, and Dr R. W. Ingle, for reading the manuscript of this paper and for many useful comments and criticisms.

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Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (figs 8a–b).
Nucula largillierti Philippi, 1861: 87
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

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Holotype

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33.51S, 25.39E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and of date.

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BRIAN KENSLEY

RECORDS OF MUD-PRAWNS (GENUS *CALLIANASSA*) FROM SOUTH AFRICA AND MAURITIUS (CRUSTACEA, DECAPODA, THALASSINIDEA)

VOLUME 69 PART 4 DECEMBER 1975 ISSN 0303-2515

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(*continued inside back cover*)

ANNALS OF THE SOUTH AFRICAN MUSEUM
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NOTES ON VARIATION IN PENGUINS AND ON FOSSIL PENGUINS FROM THE PLIOCENE OF LANGEBAANWEG, CAPE PROVINCE, SOUTH AFRICA

By

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NOTES ON VARIATION IN PENGUINS AND ON FOSSIL PENGUINS FROM THE PLIOCENE OF LANGEBAANWEG, CAPE PROVINCE, SOUTH AFRICA

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(With 5 figures and 4 tables)

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ABSTRACT

Improved statistical data on limb bones of Recent *Spheniscus demersus* agree with previous suggestions that adaptively functional elements in penguins have comparatively slight variation. These data assist in the interpretation of isolated fossil bones. Additional specimens from the Pliocene of Langebaanweg indicate that *Spheniscus predemersus* Simpson, 1971, was incorrectly referred to *Spheniscus*, and the species is placed in a new genus, *Inguza*. A second, larger species occurs at Langebaanweg, but available material does not warrant further identification or diagnosis.

CONTENTS

	PAGE
Introduction	59
Comparative data on variation in penguin limb bones	60
Fossils from Langebaanweg	63
Acknowledgements	72
References	72

INTRODUCTION

These notes consist of two parts. First, a statistical study is made of some dimensions of limb bones of *Spheniscus demersus*, not only to increase the data for variation in penguins generally, but also and particularly to broaden the basis for sorting and identifying isolated and often incomplete fossil penguin bones. Next, the considerably enlarged suite of fossil penguin bones from Langebaanweg is studied. It is reasonably sure that many of these bones, and especially a partial but characteristic tarsometatarsus, belong to the species previously described as *Spheniscus predemersus* (Simpson 1971*a*). The tarsometatarsus excludes the species from *Spheniscus* and indicates reference to a hitherto unnamed and undefined genus. That genus is technically established later in this paper after the basis for its distinction and for the reference of *predemersus* to it has been established, but to simplify things the new combination *Inguza predemersus* will be used throughout.

All fossil specimens here discussed are in the South African Museum. Reference numbers for all begin SAM–PQ–L, followed by a serial number, but for brevity they are here given only as L plus the number, which suffices for identification.

Ann. S. Afr. Mus. **69** (4), 1976: 59–72, 5 figs, 4 tables.

All measurements are in millimetres. Other conventions and abbreviations are explained as needed.

COMPARATIVE DATA ON VARIATION IN PENGUIN LIMB BONES

Many museums now have some osteological material of penguins, but few have samples of unified origin and large enough to give good estimates of population variation. The most nearly adequate statistical data are those in Simpson (1946) for specimens, mostly of *Aptenodytes patagonicus*, in the American Museum of Natural History, relatively few specimens, not sexed, and without precise locality data. Now better data can be given for another species, *Spheniscus demersus*, the African black-footed or jackass penguin.

The population represented is that of Robben and Dyer Islands, one north-west and the other south-east of Cape Town. Although the islands are some distance apart, their penguin populations are essentially unified as birds banded on one may turn up on the other. The birds in this sample were caught in an oil-slick and taken for treatment by the South African National Foundation for the Conservation of Coastal Birds (SANCCOB) but failed to survive. (Many oiled birds do recover after treatment.) The dead birds were turned over to the South African Museum, where their wing and leg bones were macerated. The left limb bones are in that Museum, and the right limb bones of the same birds were kindly sent by Dr Q. B. Hendey to the Simroe Foundation for study by the author.

It is conceivable that the sample is biased by the fact that these birds died from oiling, but that is improbable. There is no apparent reason why mortality of adult birds from oiling would be correlated with small differences in the sizes of their limb bones.

Ten of the thirty birds involved are recorded as juvenile, and these were not included in the statistics even though some of them have apparently fully ossified limb bones. Three not recorded as juvenile do not have fully adult ossification and were therefore also excluded. One specimen consisted of wings only and was excluded because it is desirable to have wing and leg measurements all on the same individual. One more was disregarded because of poor preservation and one because of pathology (exostoses on some of the bones). Nineteen specimens were thus measured. Of these, five were recorded as males, one doubtfully. The doubtful specimen does happen to be smaller than the four certain males, but it was considered incorrect to exclude it from the sample on that account. The fourteen females measured are all recorded without question as to sex.

The dimensions measured were selected primarily for their potential usefulness in judging variation and proportions in single bones, especially in fossil specimens at hand. They are as follows:

Humerus:

a. Maximum longitudinal dimension.

b. Width of shaft about one-third of distance distal to head. In this species this is taken at the minimum width of the shaft.

c. Width of shaft about two-thirds of distance distal to head.

d. From the radial condyle to the longest distal process.

Femur:

a. From the hollow between the head and trochanter to that between distal condyles.

b. Proximal width.

c. Distal width.

Tibiotarsus:

a. From the proximal articulation (excluding the crest) to the hollow between distal condyles.

b. Distal width.

Tarsometatarsus:

a. Length on third metatarsal (proximal convexity to distal groove).

b. Width of distal end of third metatarsal.

c. Length on fourth metatarsal (to distal groove).

The following statistics are given in Tables 1, 2 and 4:

N —number of specimens.
OR—observed range in sample.
$\overline{X}$ —mean and standard error.
S —Standard deviation and standard error.
V —coefficient of variation and standard error.

The males of this living species are in general larger in mean sample estimates than the females, 'humerus *d*' being the only dimension of which this is not true. However the differences are slight and there is large overlap in all the observed ranges, still more in the probable population ranges. These bones in this species cannot be reliably sexed on the basis of size.

The humerus is distinctly more variable in males than in females of this sample. That could be due to sampling error, but probably is not. Its functional significance, if any, is not clear. The tarsometatarsus is also somewhat more variable in males than in females, but here the difference is less and is quite probably due to sampling error. No sexual difference in variation is indicated for femur or tibiotarsus.

The coefficients of variation are in general quite small. The mean of the 24 coefficients in Table 1 is only 3,63. The variation in functionally adaptive dimensions of birds tends to be low, suggesting that these characters are subject to effective stabilizing or centripetal selection. It is interesting that this is true of wing bones in penguins, aqueous fliers, as well as in aerial fliers.

An aid to sorting isolated bones is provided by the ratios of measurements in associated bones of individuals of one species. Some data from the *Spheniscus demersus* sample are given in Table 2. There is no evident sexual distinction in this respect. These ratios are likely to be different in different species, but they probably will be close to those for *S. demersus* in species of approximately the same size. There is a tendency in Recent species, at least, for the humerus to be

TABLE 1

Statistics on Some Limb Bones of *Spheniscus demersus*

	N	OR	$\bar{X}$	S	V
Males					
Humerus					
a	5	64,0–69,5	67,82 ± 1,06	2,37 ± 0,75	3,50 ± 1,11
b	5	10,0–11,5	10,64 ± 0,33	0,74 ± 0,24	6,99 ± 2,21
c	5	11,7–13,4	12,44 ± 0,36	0,80 ± 0,25	6,40 ± 2,02
d	5	19,9–22,5	21,56 ± 0,50	1,12 ± 0,35	5,20 ± 1,65
Femur					
a	5	65,6–70,0	68,32 ± 0,73	1,64 ± 0,52	2,40 ± 0,76
b	5	14,5–15,5	15,04 ± 0,20	0,44 ± 0,14	2,96 ± 0,94
c	5	13,9–15,0	14,42 ± 0,22	0,50 ± 0,16	3,45 ± 1,09
Tibiotarsus					
a	5	96,7–104,4	101,16 ± 1,28	2,87 ± 0,91	2,84 ± 0,90
b	5	13,1–14,3	13,86 ± 0,21	0,46 ± 0,15	3,33 ± 1,05
Tarsometatarsus					
a	5	28,9–32,8	31,26 ± 0,66	1,47 ± 0,47	4,72 ± 1,49
b	5	6,3–7,1	6,76 ± 0,15	0,34 ± 0,11	5,08 ± 1,61
c	5	26,0–28,5	27,22 ± 0,44	0,98 ± 0,31	3,61 ± 1,14
Females					
Humerus					
a	14	63,9–69,3	66,66 ± 0,51	1,91 ± 0,36	2,87 ± 0,54
b	14	10,0–10,8	10,43 ± 0,07	0,28 ± 0,05	2,64 ± 0,50
c	14	11,3–12,7	11,94 ± 0,09	0,35 ± 0,07	2,91 ± 0,55
d	14	20,9–22,9	21,66 ± 0,14	0,51 ± 0,10	2,34 ± 0,44
Femur					
a	14	61,9–68,9	65,94 ± 0,43	1,61 ± 0,30	2,44 ± 0,46
b	14	14,1–15,5	14,79 ± 0,12	0,44 ± 0,08	3,01 ± 0,57
c	14	13,6–15,3	14,27 ± 0,12	0,45 ± 0,09	3,19 ± 0,60
Tibiotarsus					
a	14	91,8–102,6	97,54 ± 0,88	3,29 ± 0,62	3,37 ± 0,64
b	14	13,1–14,3	13,71 ± 0,11	0,42 ± 0,08	3,06 ± 0,58
Tarsometatarsus					
a	14	28,9–32,8	30,79 ± 0,28	1,05 ± 0,20	3,39 ± 0,64
b	14	6,5–7,4	6,74 ± 0,07	0,26 ± 0,05	3,93 ± 0,74
c	14	25,4–28,0	26,55 ± 0,24	0,92 ± 0,17	3,45 ± 0,65

Symbols are explained in the text.

TABLE 2

Ratios of Some Dimensions in *Spheniscus demersus*

		Humerus *a* Femur *a*			Humerus *a* Tarsometatarsus *a*			Femur *a* Tarsometatarsus *a*	
	N	OR	$\bar{X}$	N	OR	$\bar{X}$	N	OR	$\bar{X}$
Males	5	0,96–1,01	0,99	5	2,12–2,21	2,17	5	2,10–2,27	2,19
Females	14	0,98–1,04	1,01	14	2,09–2,28	2,17	14	2,08–2,27	2,14

Symbols are explained in the text.

longer relative to the femur and tarsometatarsus the larger the species (Simpson 1946: table 8).

Since limb bones cannot be sexed by size in *S. demersus* and this is apparently usually but not necessarily always true in penguins, statistics were also calculated for some dimensions in a sample of *S. demersus* with the most probable ratio of males to females, that is, equal numbers of the two sexes. This includes the five males available and five females taken at random (using a table of random numbers applied to the serial numbers of these specimens). The dimensions were selected for comparison with available specimens of fossil humeri and femora from Langebaanweg. Results are given in Table 4.

FOSSILS FROM LANGEBAANWEG

Penguins from the Pliocene of Langebaanweg were previously described by the author (Simpson 1971*a*) on the basis of three humeri, one essentially complete and two fragmentary, a partial tibiotarsus, two complete femora, and one pedal phalanx. The humeri were referred to a then new species as *Spheniscus predemersus* (Fig. 1). It will be shown below that the generic ascription was almost certainly erroneous, and the name *Inguza predemersus* will be used here.

Later discoveries have added greatly to the available materials, although even now they are not wholly adequate. Most of the bones of the wings and legs are represented, although some, unfortunately including the tarsometatarsus, only by imperfect specimens. The provenience is described in Hendey (1974) and Dr Hendey has added information in personal communication. The specimens are from the 'E' Quarry at Langebaanweg, and for the most part from the area designated as 'East Stream' (Hendey 1974: fig. 3). All are from the Varswater Formation, and with one exception they are from 'Bed 2' of Hendey (1974: table 4), which he is now proposing to call the 'Quartzose Sand Member'. That member is comprised of deposits accumulated in and adjacent to an estuary and its fauna is made up largely of terrestrial vertebrates. Besides the penguins, aquatic or amphibious elements are represented by an otter, *Enhydriodon africanus*, and a seal, *Prionodelphis capensis*. These are at present the only fossil penguins found in a predominantly non-marine association. The one exception referred to above is from the Gravel Member (=Bed 1), the basal unit of the Varswater Formation in which marine fossils are predominant.

This deposit is the type of the proposed South African provincial land mammal stage and age Langebaanian, Pliocene in age and tentatively correlated with the Astian of Europe and the Rexroadian of North America (Hendey 1974: table 8).

Renewed study of the systematics of these fossil penguins with enlarged samples is based on the humeri, femora, tibiotarsi, and tarsometatarsi. The other bones, although numerous, are less characteristic and do not add to conclusions based on these bones.

Measurements are given in Table 3. The dimensions are the same as those specified in the text above and used in Tables 1 and 2. Statistics derived from these measurements are given in Table 4 and there compared with statistics for a sample of Recent *Spheniscus demersus* made to include equal numbers of the two sexes, as noted in previous text. These dimensions, and therefore the measurements, differ somewhat from those previously used for the smaller sample (Simpson 1971*a*: table 1). For 'humerus *b*' and 'humerus *c*' the co-

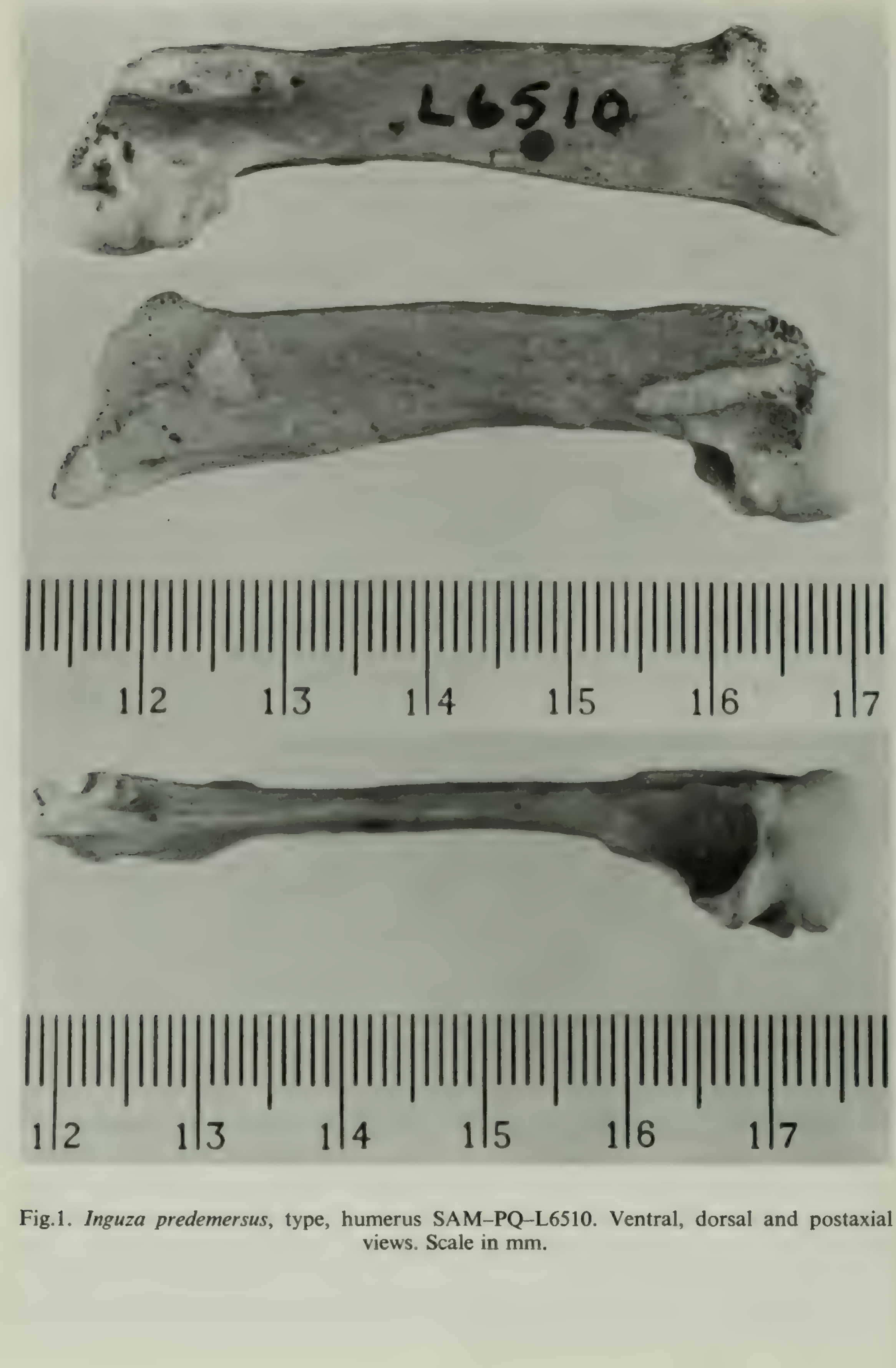

Fig.1. *Inguza predemersus*, type, humerus SAM–PQ–L6510. Ventral, dorsal and postaxial views. Scale in mm.

TABLE 3

Measurements of some Limb Bones of Fossil Penguins from Langebaanweg

Specimen No.	Dimension			
	Humerus			
	a	*b*	*c*	*d*
L6510, holotype of *Inguza predemersus*	59,0	8,6	10,0	17,8
L123010	57,5	9,6	10,9	18,9
L14853	—	8,7	11,1	18,4
L12887A	—	9,4	11,7	19,3
L22952	—	10,0	11,2	—
L21928	—	9,8	—	—
	Femur			
	a	*b*	*c*	
L23002	59,8	—	13,3	
L22983	61,5	—	13,4	
L22117	62,3	13,9	13,9	
L122954	—	14,4	—	
L12524A	—	—	14,5	
L13154	75,1	18,1	16,3	
L3656	79,5	—	17,6	
L13066A	—	18,7	—	
	Tibiotarsus			
	a	*b*		
L23012	85,2	11,5		
L22950	ca. 92	12,3		
	Tarsometatarsus			
	a	*b*	*c*	
L23018	27,2	5,3	24,2	
L22974	—	4,7	—	
L22985	—	ca. 7½	—	

Symbols are explained in the text.

TABLE 4

Some Statistical Data on a Sample with Equal Numbers of Males and Females of *Spheniscus demersus* and on Available Fossils from Langebaanweg

Sample	Dimension	N	OR	$\overline{X}$	S	V
Spheniscus demersus	Humerus *b*	10	10,0–11,5	10,59 ± 0,16	0,52 ± 0,12	4,87 ± 1,09
	Humerus *c*	10	11,7–13,4	12,24 ± 0,16	0,62 ± 0,12	4,21 ± 0,94
	Humerus *d*	10	19,9–22,5	21,63 ± 0,25	0,80 ± 0,18	3,72 ± 0,83
	Femur *a*	10	61,9–70,0	66,63 ± 0,79	2,50 ± 0,56	3,76 ± 0,84
	Femur *c*	10	13,6–15,0	14,19 ± 0,14	0,44 ± 0,10	3,12 ± 0,70
Inguza predemersus	Humerus *b*	6	8,6–10,0	9,35 ± 0,24	0,58 ± 0,17	6,19 ± 1,79
	Humerus *c*	5	10,0–11,7	10,98 ± 0,28	0,62 ± 0,29	5,67 ± 1,27
	Humerus *d*	4	17,8–19,3	18,60 ± 0,32	0,65 ± 0,23	3,48 ± 1,23
	Femur *a*	3	59,8–62,3	61,20 ± 0,74	1,28 ± 0,52	2,09 ± 0,85
	Femur *c*	4	13,3–14,5	13,78 ± 0,28	0,55 ± 0,19	7,26 ± 2,57
Mixed sample, all measureable bones from Langebaanweg						
	Femur *a*	5	59,8–79,5	67,64 ± 4,02	9,00 ± 2,01	13,31 ± 2,98
	Femur *c*	6	13,3–17,6	14,83 ± 0,71	1,74 ± 0,50	11,75 ± 3,39

Symbols are explained in the text.

efficients of variation are somewhat higher than for *S. demersus* or, so far as data are available, most other Recent penguins. However the difference is not great enough to indicate that it is probably not due either to sampling error or to somewhat greater real variability within a single species. For 'humerus *d*', generally a less variable dimension, V is not statistically different from that of *S. demersus*. Except for the moderate variation in these dimensions and in the ratios among them, these humeri do not differ appreciably in morphology. They are therefore all tentatively referred to *Inguza predemersus*, the more common but, as will now appear, not the only species of penguins in this fauna.

There are seven tibiotarsi in the collection but only one is complete, and although three others are nearly so only one other gives approximate comparable measurements. The variation in size is considerable, but again not enough to indicate reliably that more than one species is represented. The two most complete specimens, L23012 and L22950, are within a size range appropriate for association with humeri referred to *Inguza predemersus*.

The situation regarding the femora is quite different. For the six femora affording one or more useful measurements the coefficients of variation for all taken together are decidedly too high to be derived from a single species of penguins. It is also evident in Table 3 that they fall into two quite distinct size groups. The smaller group, L23002, L22983, L22117, L22954 and L12524A, is of appropriate size for association with the humeri referred to *Inguza predemersus* (Fig. 2). The ratio of the mean for 'humerus *a*' (two specimens) to the mean for 'femur *a*' (three specimens) is 0,95. In *Spheniscus demersus* it is 0,99 (Table 2), not significantly different. The femora L13154 and L3656 give a corresponding ratio of 0,75, which is significantly different, and these femora surely belong to a second, larger species, to which L13066 also belongs (Fig. 3).

'Femur *a*' for specimens referred to *Inguza predemersus* has unusually slight variation and 'femur *c*' unusually large variation. However N is small for both (3 and 4, respectively), standard errors are correspondingly large, and the differences of values of V from those found in *Spheniscus demersus* are not significant.

The specimen mentioned above as having come from the Gravel Member is L21628, the distal part of a femur. The end is too abraded or corroded for useful measurement, but this bone agrees closely with the larger specimens from the Quartzose Sand Member. Dr Hendey (pers. com.) notes that 'The Gravel Member does include derived fossils, probably of Miocene Age'. It is, however, probable that this fragment represents the same species as the larger one in the overlying member.

There are 16 partial tarsometatarsi in the collection, but most of these are scraps, especially distal condyles, from which little can be learned. The most extensive, L23018 (Fig. 4), includes the third and fourth tarsometatarsals and the dorsal, but not the plantar, part of the proximal end. The ratio for mean 'humerus *a*' of two *Inguza predemersus* to 'tarsometatarsus *a*' of this specimen is 2,14, which suggests that these animals were of quite closely the same size

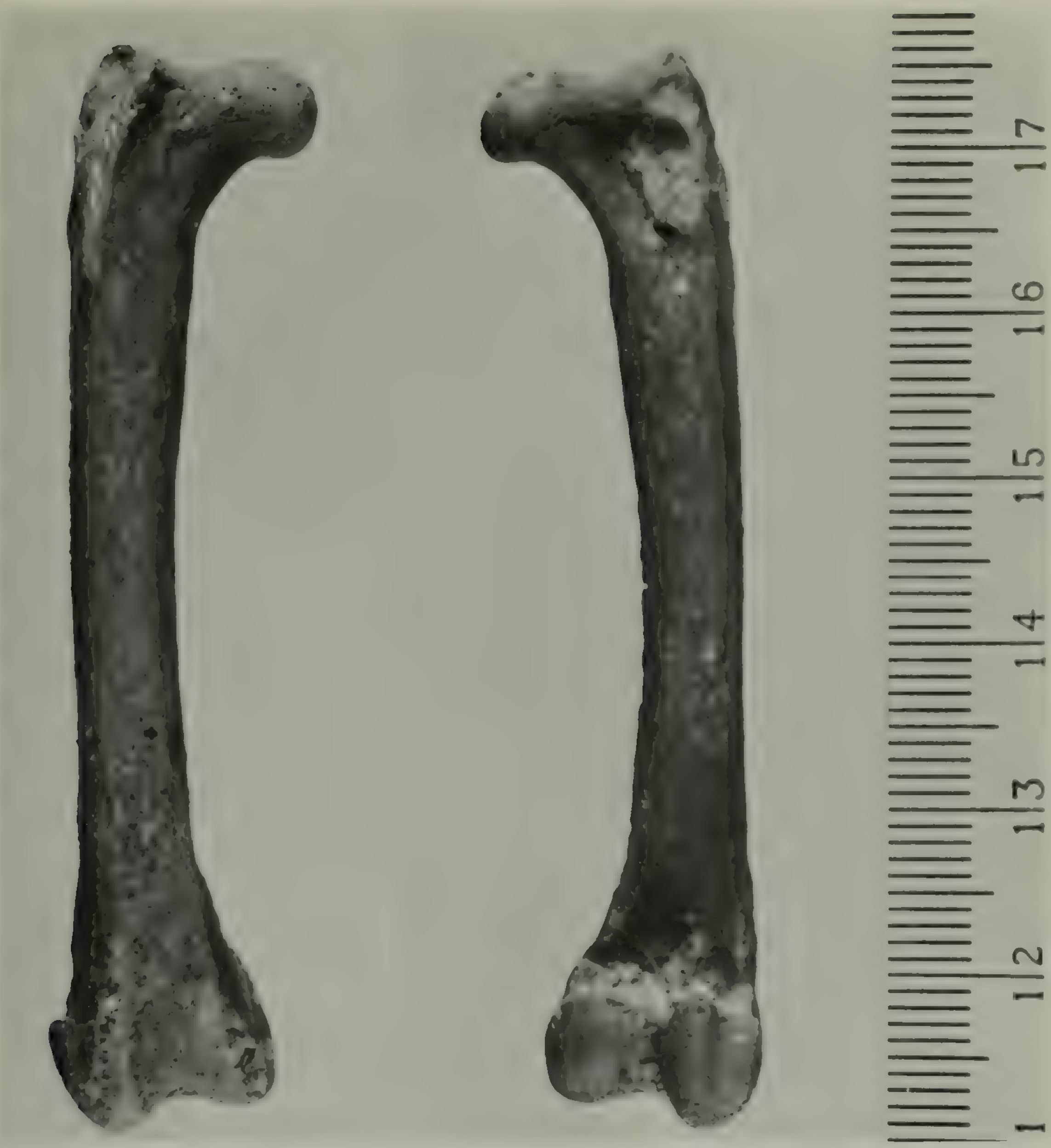

Fig. 2. *Inguza predemersus*, femur SAM–PQ–L22117. Anterior and posterior views.

and very likely of the same species. L23401, a fourth tarsometatarsal with some adjacent bone, and L22974, most of a third tarsometatarsal with some adjacent bone, also may be referred to this species, to which most of the lesser fragments probably belong. There are, however, some scraps, notably L22985, the distal part of the third tarsometatarsal and some adjacent bone, and L23402, approximately the same but even more poorly preserved, which belong to a definitely distinct and larger species (Fig. 5). The species could well be the same as that represented by the larger femora.

On L23018 it can be determined that the medial intermetatarsal foramen (or inner proximal foramen of Zusi 1975) is larger than the lateral foramen and slightly more distal. It opens on the plantar side distal to the medial (inner)

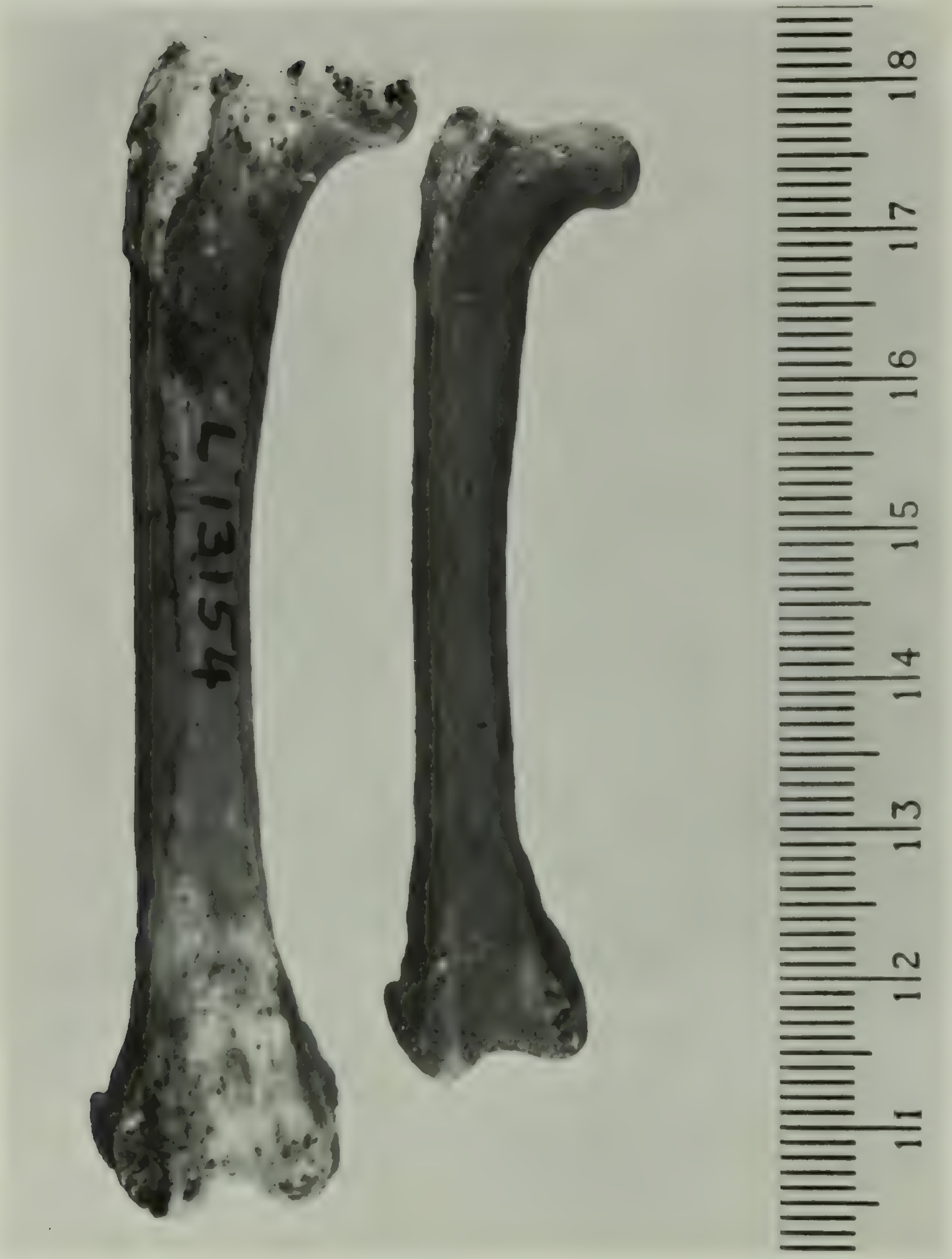

Fig. 3. Spheniscidae indet. (left) and *Inguza predemersus* (right), femora SAM–PQ–L13154 and SAM–PQ–L22117. Anterior views.

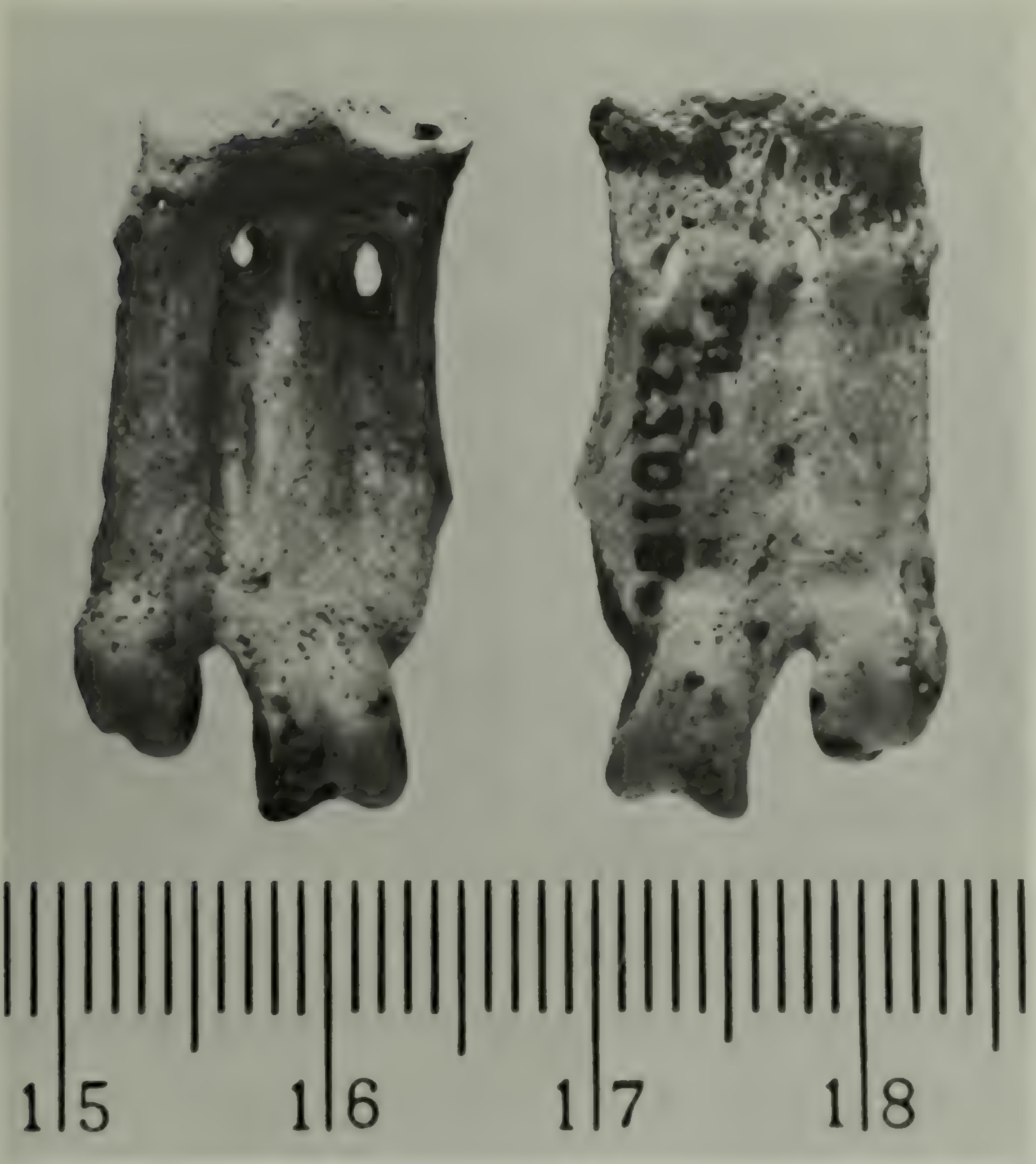

Fig. 4. *Inguza predemersus*, tarsometatarsus SAM–PQ–L23018. Dorsal and plantar views.

calcaneal ridge. These characters definitely exclude reference to the genus *Spheniscus* in which the medial foramen is relatively smaller, is somewhat more proximal, and opens on the medial side of the medial calcaneal ridge. (See Zusi 1975, who shows that the latter arrangement occurs in *Eudyptes*; I have confirmed that it also occurs and is apparently invariable in *Spheniscus demersus*.) Among Recent penguins the genera *Aptenodytes* and *Pygoscelis* have the arrangement of intermetatarsal foramina more as in this fossil. The Recent species of those genera are decidedly larger than the fossil, even in *Pygoscelis*. The tarsometatarsus is also less elongate, the foramina relatively less proximal,

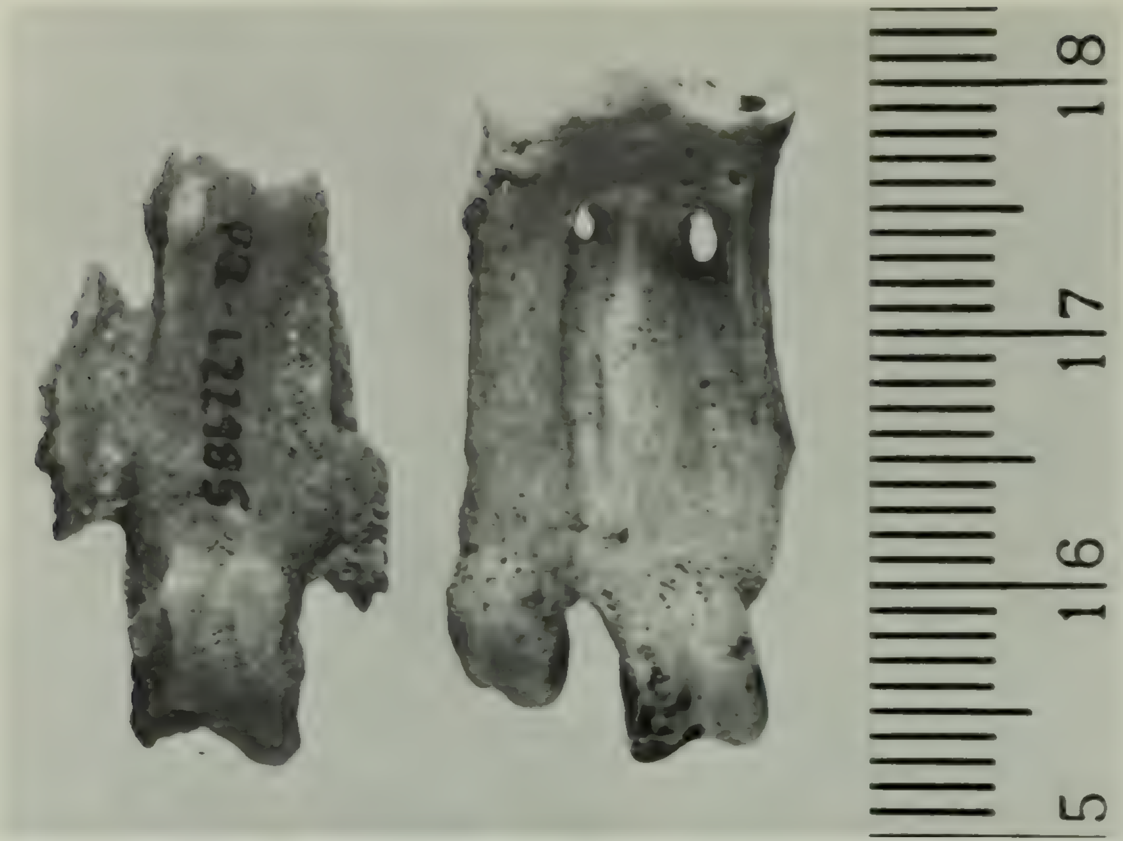

Fig. 5. Spheniscidae indet. (left) and *Inguza predemersus* (right), tarsometatarsi SAM–PQ–L22985 and SAM–PQ–L23018. Dorsal views.

more nearly in a transverse line, and more nearly equal in size. Reference of the fossil to *Pygoscelis* or *Aptenodytes* is not tenable.

It seems open to little question that the holotype humerus of *Inguza predemersus*, originally referred to *Spheniscus*, and the tarsometatarsus, now available and added to the hypodigm, belong to the same species and that the species neither belongs in nor was ancestral to *Spheniscus*. The humerus really differs little from that of *Spheniscus demersus*. Apart from smaller size, it has the shaft slightly more sigmoid and it lacks a preaxial angle or tubercle; it now follows that these slight differences are associated with a tarsometatarsus surely generically distinct from *Spheniscus*. They therefore now appear to be generic characters although that would hardly be tenable on the basis of the humeri alone. The author has been unable to find a previously named extinct genus to which this species can be reasonably referred. *Duntroonornis* from the early Oligocene of New Zealand may come as close as any, but its less elongate tarsometatarsus, smaller and more unequal foramina, and perhaps the obliquity of the metatarsals, if that is not caused by crushing of the only known specimen, distinguish it (see Simpson 1971*b*). '*Spheniscus*' *predemersus* must therefore be referred to a new, extinct genus which will now be formally proposed. It is improbable that this genus is ancestral or close to any living penguins, but it may conjecturally have some special relationship with *Pygoscelis* or perhaps even *Aptenodytes*.

It is probably impossible and certainly inadvisable to identify or name the second, larger species from Langebaanweg on the basis of specimens now in hand. It is certainly distinct from *Inguza predemersus*, but the available specimens are otherwise not diagnostic.

Technical validation of the new generic name and revision of the specific name follow.

Order SPHENISCIFORMES

Family **Spheniscidae**

Inguza, gen. n.

Etymology: 'Inguza' is given by McLachlan & Liversidge (1970) as a 'native [South African] name' for penguins. Greek derivatives appropriate for penguins have become rather overdone and repetitious. Native African languages do not have gender in the Latin sense, so this name is arbitrarily designated as masculine.

Type-species: Spheniscus predemersus Simpson, 1971.

Included species: Type only.

Known distribution: Langebaanian, Pliocene, in the Quartzose Sand Member of the Varswater Formation at Langebaanweg, Cape Province, Republic of South Africa.

Diagnosis: Humerus with shaft narrower proximally, somewhat sigmoid; tricipital fossa strongly bipartite; preaxial angulation absent. Tarsometatarsus elongate; intermetatarsal foramina proximal; medial foramen larger than lateral foramen, slightly more distal, opening distal to the medial calcaneal ridge on the plantar surface; third and fourth metatarsals straight.

Inguza predemersus (Simpson, 1971)

Spheniscus predemersus Simpson, 1971*a*: 1144.

Etymology: Pre+ demersus, as older than known *Spheniscus demersus* and erroneously believed to be specially related to the latter.

Holotype: SAM–PQ–L6510, left humerus, essentially complete.

Present Hypodigm: The type and the following:

L23010, complete humerus, L14853, L12887A, L22952, and L21928, partial humeri.

L22117A, complete femur, L23002, L22983, L122954, and L12524A, partial femora.

L23012, complete, and L22930, nearly complete, tibiotarsi.

L23018 and L22974, partial tarsometatarsi.

Numerous other bones, mostly fragmentary, almost certainly belong to this species but have not yet entered explicitly into the present concepts and diagnoses of the genus and species.

Known distribution: As for the genus.

Diagnosis: Only known species of *Inguza*. Measurements in Table 3.

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The illustrations are by Mr S. Kannemeyer of the South African Museum.

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*This study also refers to bones other than the skull.

6. SYSTEMATIC papers must conform with the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. n., sp. n., comb. n., syn. n., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (*Lembulus*) *bicuspidata* (Gould, 1845)

Figs 14–15A

Nucula (*Leda*) *bicuspidata* Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (figs 8a–b).
Nucula largillierti Philippi, 1861: 87
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:
comma separates author's name and year
semicolon separates more than one reference by the same author
full stop separates references by different authors
figures of plates are enclosed in parentheses to distinguish them from text-figures
dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33.51S, 25.39E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and of date.

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'. . . in *C. namacolus* (Fig. 10) . . .'

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Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as
'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

GEORGE GAYLORD SIMPSON

NOTES ON VARIATION IN PENGUINS AND ON FOSSIL PENGUINS FROM THE PLIOCENE OF LANGEBAANWEG, CAPE PROVINCE, SOUTH AFRICA

VOLUME 69 PART 5 MARCH 1976 ISSN 0303-2515

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FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines.—*Archs Zool. exp. gén.* **74**: 627–634.
KOHN, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon.—*Ann. Mag. nat. Hist.* (13) **2**: 309–320.
KOHN, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean.—*Bull. Bingham oceanogr. Coll.* **17** (4): 1–51.
THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* **4**: 269–270. Jena: Fischer.—*Denkschr. med.-naturw. Ges. Jena* **16**: 269–270.

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ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

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LEISTOCENE HISTORY AND COASTAL MORPHOLOGY OF THE YSTERFONTEIN–ELANDS BAY AREA, CAPE PROVINCE

By

ANTHONY J. TANKARD

Cape Town Kaapstad

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PLEISTOCENE HISTORY AND COASTAL MORPHOLOGY OF THE YSTERFONTEIN–ELANDS BAY AREA, CAPE PROVINCE

By

ANTHONY J. TANKARD

South African Museum, Cape Town

(With 25 figures and 3 tables)

[*MS accepted 4 September 1975*]

ABSTRACT

The south-western Cape has been unstable throughout the Neogene and much of the Pleistocene so that an Early Pleistocene shoreline at 10 m a.s.l. correlates with the 45–50 m transgression complex of the Namaqualand coast. There were three sea-level peaks in the last interglacial: at 6,3 m a.s.l., 2–3,5 m a.s.l., and 0 m a.s.l. which are correlated with the Tyrrhenian II and Tyrrhenian I of Mallorca. No evidence was found of Holocene sea levels much higher than the present. The Weichselian lowering of sea level was accompanied by maximum dune activity.

CONTENTS

	PAGE
Introduction	73
Regional geomorphology and pre-Pleistocene geology	75
Tectonic setting	77
Early Pleistocene marine deposits	80
The 13 m shoreline	84
Late Pleistocene marine history	84
Open-coast facies	85
Rocky shores	85
Exposed sandy shores	87
Estuarine-lagoonal facies	98
Verlorevlei	98
Berg River	99
Saldanha Bay	102
Langebaan Lagoon	103
Age of the deposits	109
Recent	110
Fluvial sediments	110
Aeolianites	113
Proposed new lithostratigraphic names	114
Conclusions and synthesis	114
Acknowledgments	116
References	117

INTRODUCTION

The late Cenozoic history of the South African coast is related to the history of the sea level. In the Pleistocene sea level fluctuated in sympathy with the repeated waxing and waning of northern hemisphere ice sheets, and palaeogeographic studies show that coastal lowlands all over the world have been subjected to periods of alternating submergence and emergence.

Ann. S. Afr. Mus. **69** (5), 1976: 73–119, 25 figs, 3 tables.

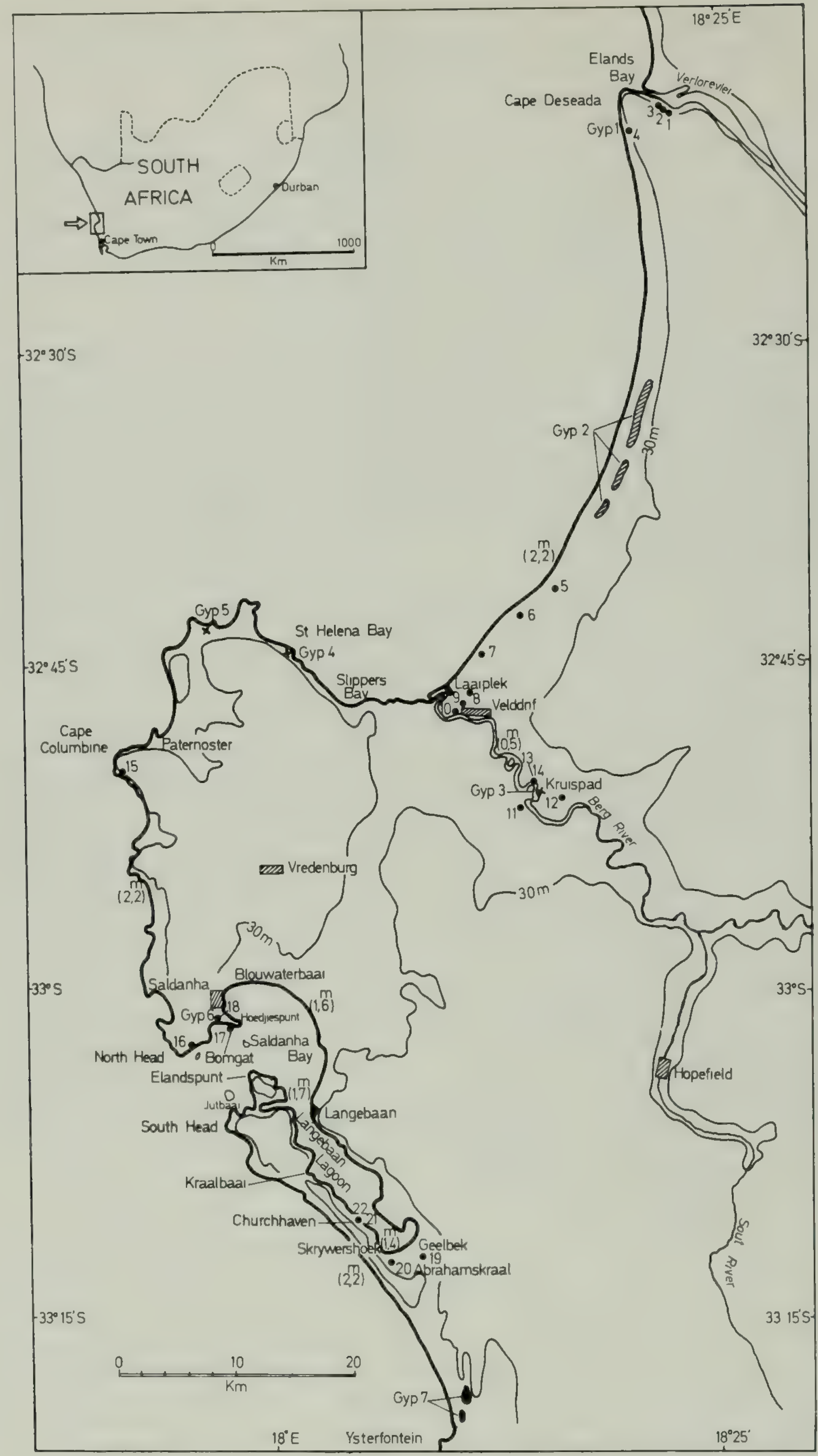

Fig. 1. Locality map showing sampling sites (solid circles). Tidal range is shown in brackets; evaporite deposits are referred to as 'Gyp'.

Previous literature on the Pleistocene marine history of the coastal areas of the south-western Cape is limited to a few texts, mostly of a geomorphic nature. Krige (1927) published the first major study. He found evidence for two general emergences: shorelines at 15–18 m he called the Major Emergence, and those at 6–9 m the Minor Emergence, which was thought to be of Recent origin. In the Saldanha area he identified the Major Emergence at 6–12 m and proposed that the area had been downwarped. Haughton (1931) briefly described the geology and palaeontology. Mabbutt (1956, 1957) claimed marine terraces at 91 m, 45–60 m, 20 m, 13 m, 9 m, and 7,5 m a.s.l. (above mean sea level). All of the terraces above 9 m he identified as marine terraces on the basis of flattish surfaces. The most detailed geological approach to the problem has been that of Parker (1968). Davies (1973) found evidence of transgressions to 9 m a.s.l. (Eem) and 1,5 m a.s.l. (Recent).

This paper describes the results of an investigation into the Pleistocene history of the coastal area between Elands Bay and Ysterfontein (Fig. 1). All altitudes are recorded as height above mean sea level (a.s.l.). Tidal amplitudes are shown in Figure 1. Mean wave height is 3 m, and the highest recorded waves were 9,5 m (Pomeroy 1965). Ocean swell is predominantly south-westerly. Terms such as 'last interglacial', 'last glacial', 'Eem', 'Weichselian', etc. are used purely as time units based on European glacial events.

REGIONAL GEOMORPHOLOGY AND PRE-PLEISTOCENE GEOLOGY

The south-western Cape has a Mediterranean-type climate with hot, dry summers and mild winters. The temperature range at Cape Columbine is 19–11°C. Average annual rainfall is 262 mm with a winter maximum. The coastal waters have a temperature range of 13–15°C (Shannon 1966). The west coast is characterized by active upwelling of cold subsurface water in the summer months. An evergreen Cape Macchia vegetation predominates and grasses are rare so that the surface is never adequately protected against wind erosion. Soils are generally skeletal.

A lowlying area, drained by the Berg River and its tributaries, lies between the Hottentots Holland Mountains and the Atlantic Ocean, and reaches a width of 110 km at latitude 33°S. The higher eastern part of this lowland is known as the Swartland, and the lower western part as the Sandveld. It has been suggested (Talbot 1947; Mabbutt 1956) that the Swartland was planed by a shallow sea during the Pleistocene. Other than its plain-like surface there is no evidence to support this claim. The Swartland and Sandveld are characterized by thick accumulations of Late Pleistocene and Recent dune sands. Typical of an aeolian landscape, the Sout River has many ponds and marshes.

The pre-Tertiary geology (Fig. 2) comprises rocks of latest Precambrian and Early Palaeozoic age. The oldest rock assemblage, the geosynclinical Malmesbury Group, consists of fine-grained greywackes and slates with associated phyllites, quartzites, and felspathic grits (Truswell 1970). On the farm

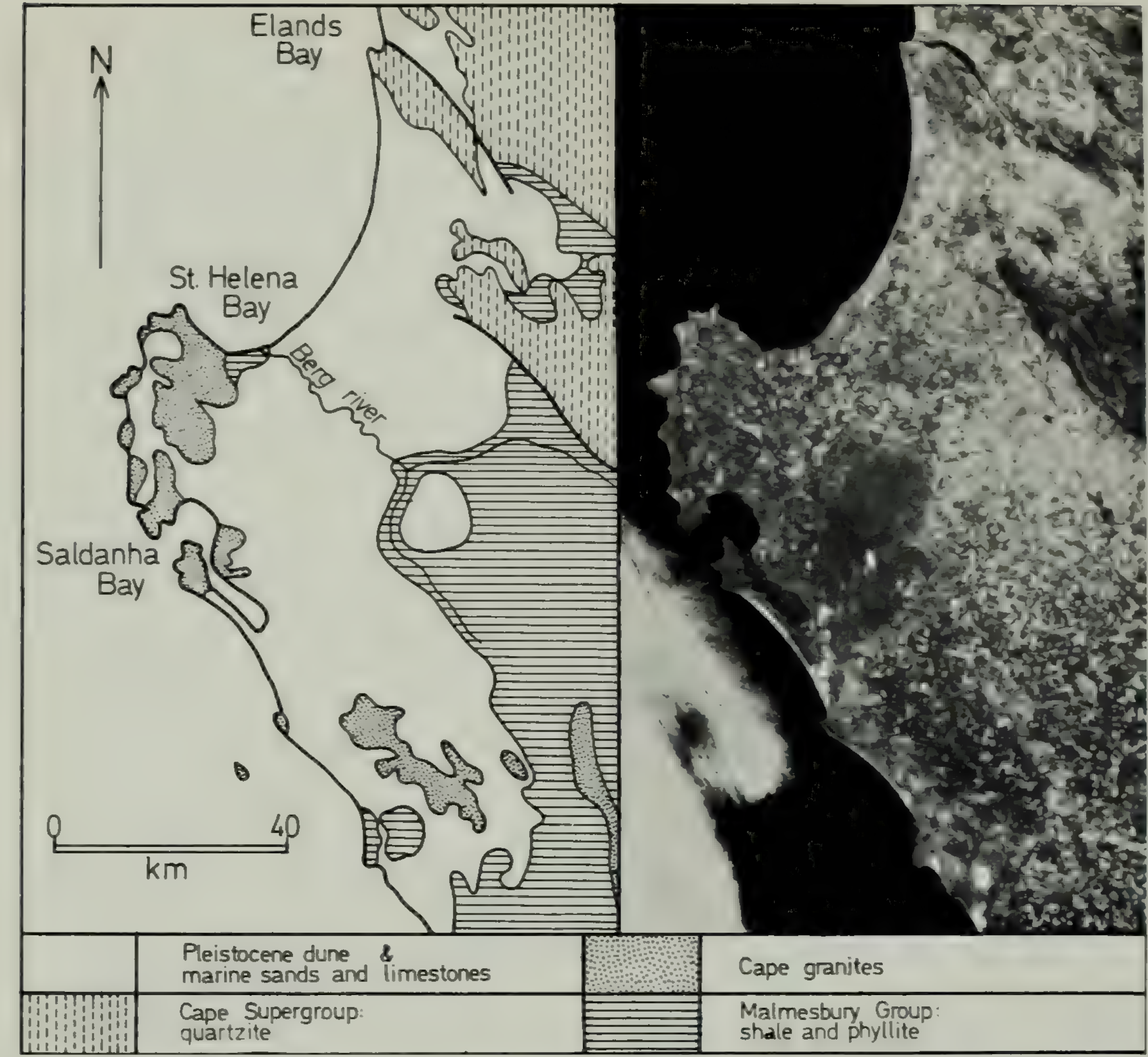
Elands Bay
N
St. Helena Bay
Berg river
Saldanha Bay
0
40
km
Pleistocene dune & marine sands and limestones
Cape granites
Cape Supergroup: quartzite
Malmesbury Group: shale and phyllite

Fig. 2. Comparison of geological map with ERTS–1 photograph shows the effect of lithology on topography.

Drommelvlei north of Hopefield (32.46 S, 18.25 E) a local consortium drilling for oil penetrated 3 300 m of subhorizontally bedded shales and siltstones without reaching the base. In the earliest Cambrian granites were emplaced into the core of the Malmesbury anticline in two phases of similar age. The earlier phase of intrusion is marked by a medium- to coarse-grained biotite granite, and is followed by a finer-grained quartz-porphyry. There are diorites with gabbro xenoliths at Ysterfontein.

The Cape Supergroup generally follows unconformably upon the Malmesbury Group and the Cape Granites. In the study area the Cape Supergroup mainly comprises mature conglomeratic sandstones overlying red thinly bedded siltstones, shales and sandstones which are exposed along the southern shore of Verlorevlei.

Tertiary strata consist of sediments deposited during transgressions in the Miocene and Pliocene. The Miocene Saldanha Formation consists of microsphorite and phosphatic sandstone. The Pliocene Varswater Formation comprises marine sands and gravels, pelletal phosphoritic sands, and estuarine and fluviatile sands, silts, and peats, with a rich mammalian fauna (Tankard 1974 and in press).

Figure 2 shows the influence of rock type on the regional geomorphology, where the geology is compared with an ERTS-1 satellite photograph. The western part of the area is marked by the north-west trending Darling and Vredenburg plutons which form a hilly terrain. In the north and east the resistant Cape Supergroup rocks form mountain ranges. From Elands Bay the conglomeratic sandstones form a south-east trending range which forms a natural groyne at Cape Deseada. The northern boundary of this sandstone block is a fault-scarp. Less resistant Malmesbury rocks form a negative relief. The Berg River follows the strike of the Malmesbury geosyncline. Whereas the granite and sandstone feature rocky shores, the St. Helena Bay coastline on the Malmesbury Group is entirely sandy. That Malmesbury rock underlies this entire low coastal plain is shown by the frequent inclusions of that rock in the Pleistocene marine deposits between Slippers Bay and Cape Deseada.

From a point only 28 km west of Cape Columbine and trending south-south-west is the Cape submarine canyon (Simpson & Forder 1968). This canyon has probably affected sedimentation along the St. Helena Bay coastline by acting as a sediment drain.

TECTONIC SETTING

Several lines of evidence prompt the conclusion that the west coast of the Cape Province was probably more unstable than the south coast in the Cenozoic. The Agulhas Arch forms a divide between the broad and gently sloping continental shelf to the east where the continental margin is controlled by transform faulting, and the narrow and steeply sloping shelf to the west where tensional faulting has been the controlling factor (Dingle & Scrutton 1974). The shelf break east of the Agulhas Arch is at a normal depth, lying between 120 and 180 m (Dingle 1973*a*). West of the Agulhas Arch the nature of the shelf break is variable. West of the Cape Peninsula it has an average depth of 450 m, but west of the Orange River a depth of 200 m (Dingle 1973*b*). The west coast shelf break is one of the deepest in the world (Shepard 1963). Simpson (1971) noted the variation in depth of the west coast shelf break and attributed it to differential warping of the continental margin. A double shelf break which appears in places off the west coast (Fig. 3) and which was apparently in existence during late Lower Tertiary times (Dingle 1973*b*) suggests a long history of instability.

The Agulhas Arch is a NW–SE striking antiform (Dingle 1973*a*) coinciding with the structural trend (NNW) of Late Precambrian origin. Early Tertiary intrusive dykes follow these same structural trends (Kröner 1973). On the farm Dikdoorn on the Groen River an intrusive melilite basalt has been dated at 38,5 million years old (ZSA 56). In the Bogenfels area of South West Africa

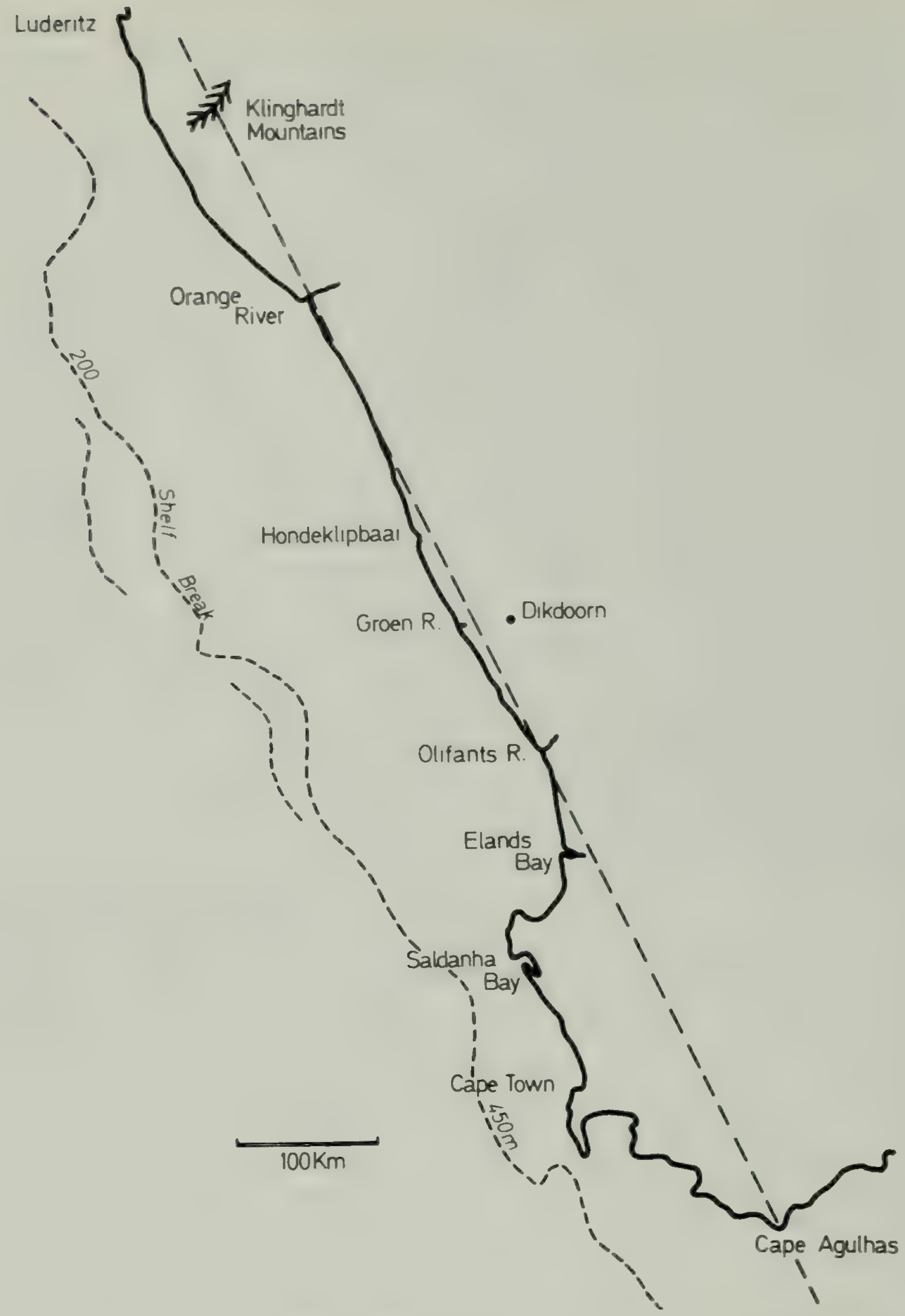

Fig. 3. Coastline configuration relative to tilt-axis. Note deep shelf-break which also deepens to the south.

phonolitic lavas of the Klinghardt volcanism have been dated at 35,7 million years old (ZSA 53). Early Tertiary igneous intrusives are also encountered offshore on the Agulhas Arch (Dingle & Gentle 1972).

Tilting probably took place about an axis or 'hinge line' which tended to follow the NNW Precambrian structural lineament and continued through the Agulhas Arch. The relative position of the 'hinge line' has been drawn in

Figure 3 by connecting the Agulhas intrusives with the Klinghardt extrusives. The axis passes west of the Dikdoorn intrusives. In reality there probably would not have been a simple well-defined 'hinge line' but rather an axial-zone about which tilting and differential warping would have taken place. It is suggested that such tilting and warping west of the axis have lowered the shelf break to abnormal depths. If the shelf west of the Agulhas Arch has tilted in relation to that east of it, it would be expected that the sedimentation to the west would be the more complex. Dingle (1971*a*, 1973*a*, 1973*b*) has shown just that. He has subdivided the Tertiary succession on both shelves by correlation of unconformities which he recognized on seismic reflection profiles. A major intra-Tertiary unconformity separates Lower from Upper Tertiary on both shelves. In addition Dingle (1973*b*) found that the Upper Tertiary of the west shelf is further subdivisible by an unconformity into lower T3 beds (upper middle Miocene) and upper T4 beds (Pliocene).

Examination of onshore Neogene sediments between Cape Town and Saldanha has confirmed Dingle's subdivision of the shelf succession. Tankard (1974) has documented Middle Miocene deposits overlain unconformably by Pliocene deposits. These Miocene deposits could possibly be attributed to a marine transgression which resulted from accretion of mid-ocean ridges at that time (Tankard in press). Regression of the high Middle Miocene sea continued through the Late Miocene and Pliocene, and the transgression complex sediments were for a time subaerially exposed. But tilting again dropped the area below sea level, causing a local transgression during a time of world-wide regression. This second transgression resulted in the accumulation of the Pliocene Varswater Formation.

Tankard (in press) noted that Neogene sediments have beach zones ranging in altitude from 9 m a.s.l. at Ysterplaat (Cape Town) to 56 m a.s.l. in the Saldanha area. But northwards in South West Africa and eastwards along the Cape south and east coasts, Tertiary marine strata are found at considerably higher elevations, suggesting relative sagging and tilting of the Cape west coast since the Miocene. The highest Pleistocene marine sediments in the Saldanha area are now at 10 m a.s.l. The highest beaches in Namaqualand are at 98 m a.s.l. (Carrington & Kensley 1969). Furthermore, the mollusc fauna from the Saldanha 10 m beach correlates most closely with that of the 45–50 m transgression complex of the Namaqualand coast north of Hondeklip Bay. This fauna includes: *Fissurella robusta*, *Purpura praecingulata*, *Triumphis dilemma*, the large *Perna perna*, and *Petricola prava*.

Tilting about the 'hinge line' shown in Figure 3 readily explains the lower elevation of the Early Pleistocene shoreline in the Saldanha area. Between the Olifants River mouth and Cape Agulhas the coastline forms a 'bulge', and the coastline between Cape Town and Saldanha is parallel to and furthest removed from the axis, so that for any degree of tilting shorelines in this area would be found at lower elevations than those north of the Olifants River where the coastline and axis almost coincide. Tilting alone would not affect elevation of the raised beaches north of the Olifants River much, but differential warping, and the local position of the axis certainly could displace them.

Dingle (1973*b*) has shown the existence of an outer shelf bar (T3) on the edge of the west coast continental shelf. Assuming that this bar formed close to sea level, it is possible to compute approximate rates of sinking since the end of the Miocene. Dingle calculated a rate of sinking 1 m/27 000 years west of the Orange River, and 1 m/12 000 years west of the Olifants River. If the 10 m beach at Saldanha is equivalent to the 45–50 m transgression complex on the Namaqualand coast, and is of a late Early Pleistocene age, say 1 million years, an approximate and average rate of sinking since that time can be computed. The average rate of subsidence at a distance from the axis equivalent to that of the shelf edge west of the Olifants River is 1 m/13 000 years. This agrees well with Dingle's estimate since the Miocene. The fact that last interglacial shorelines on the west coast show little variation from the Late Pleistocene 7 m datum implies that subsidence has either been episodic or has been operating at a decreasing rate. Little, if any, subsidence has occurred in the last 120 000–130 000 years.

To summarize: volcanic activity from the Agulhas Arch to South West Africa in the Late Eocene/Early Oligocene shows instability at least in the Early Tertiary. Tilting of the west coast relative to the south coast has resulted in a deeper shelf break in the west, and a more complex sedimentary history. The effect of tilting on onshore deposits is maximized in the Saldanha area which is furthest removed from the 'hinge line'. Although tilting has taken place since the Early Tertiary, and although post-Miocene and post-Early Pleistocene rates of subsidence appear to be in agreement, field evidence suggests that the west coast has been essentially stable in the Late Pleistocene. The southward deepening shelf break suggests that the rate of subsidence has been greatest in the south. Russell (1964) believes that most of the South African coastline is unstable.

EARLY PLEISTOCENE MARINE DEPOSITS

Deposits of presumed Early Pleistocene age occur sporadically around Saldanha Bay: on either side of Hoedjiespunt peninsula, Elandspunt, and 2,1 km north-east of Langebaan (Fig. 1). The underlying platform on Hoedjiespunt is uneven, ranging in elevation from 6,2 m to 8,9 m a.s.l. At the Bomgat on Hoedjiespunt peninsula the Early Pleistocene deposit is separated from the granite floor by a lens of Miocene microsphorite which occupies a bedrock depression. The contact between the microsphorite and the limestone is an erosional one. On the South Head, at Elandspunt, the eroded uneven surface of the granite is at 7 m a.s.l. The Early Pleistocene deposit north of Langebaan rests on the surface of an older marine limestone which is probably of Neogene age (not an aeolianite as thought by Davies (1973)). Here the contact is at

9,5 m a.s.l. A terrace at the same altitude may indicate a greater lateral extent of the Early Pleistocene deposits in the Langebaan area.

The relationship of the Early Pleistocene marine limestone at the Bomgat to the underlying microsphorite and the overlying Langebaan limestone is shown in Figure 4. The limestone contains wave-generated granite boulders at the base of 1,5 m of coquina. The matrix consists of micrite, which indicates a sheltered environment. Although articulated *Perna perna* would also suggest a sheltered environment, much fragmented shell debris is indicative of periods of higher energy marine conditions. Parker (1968) found that calcareous material constituted more than 95 per cent of the limestone.

The base of the marine limestone on the northern side of Hoedjiespunt peninsula (behind the Sea Harvest factory) is characterized by wave-generated granite boulders. The limestone consists partly of unconsolidated shell deposits, and partly of coquina and microcoquina. The marine limestone is overlain by approximately 20 m of aeolian limestone. The microcoquina is a medium-grained skeletal lime grainstone with a drusy calcite cement. Detrital shell grains form in excess of 95 per cent of the rock, and the remainder is quartz. The quartz and shell grains are generally well rounded but corroded. The shell grains include foraminifer and echinoid spine fragments. Although the lime-

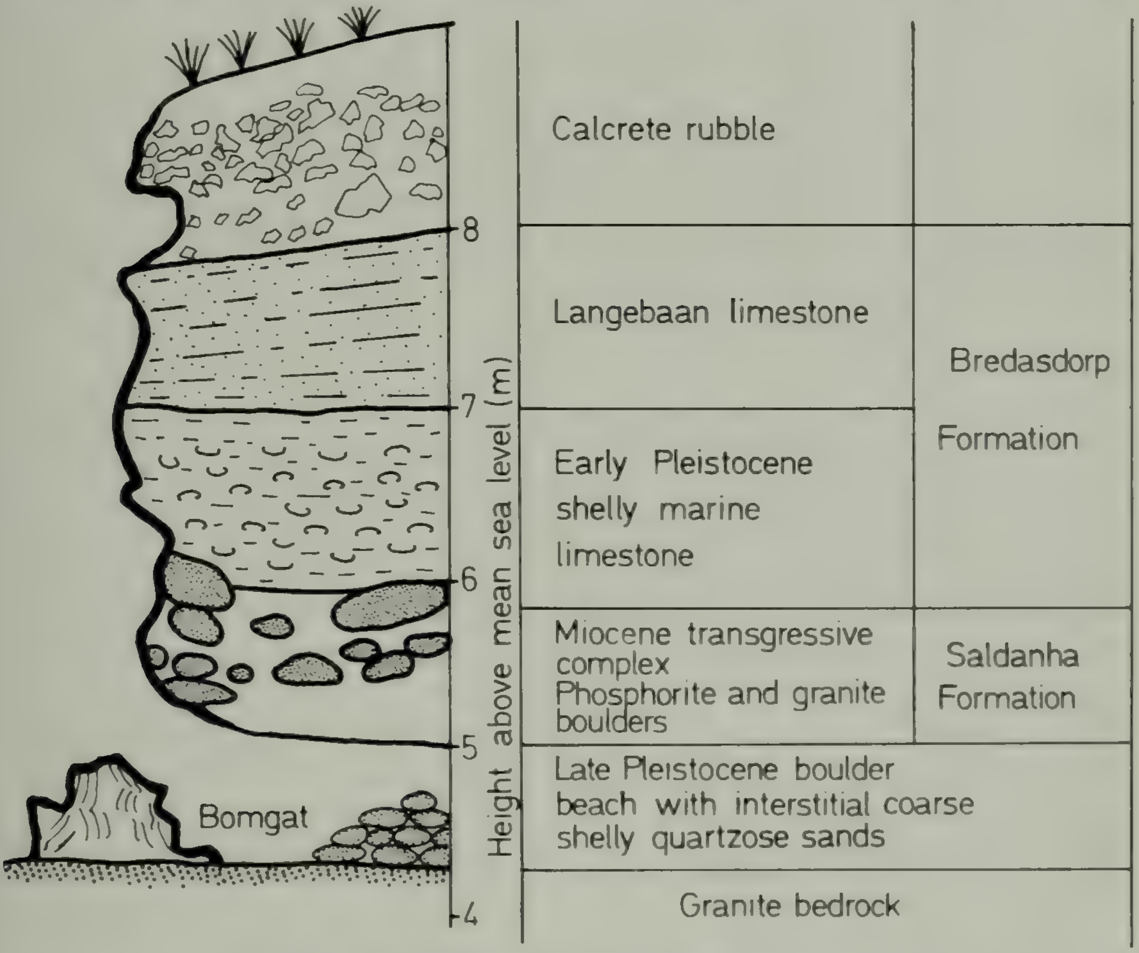
Calcrete rubble
8
Langebaan limestone
Bredasdorp Formation
7
Early Pleistocene shelly marine limestone
6
Miocene transgressive complex Phosphorite and granite boulders
Saldanha Formation
5
Bomgat
Late Pleistocene boulder beach with interstitial coarse shelly quartzose sands
Height above mean sea level (m)
4
Granite bedrock

Fig. 4. Geological section at Bomgat, Hoedjiespunt.

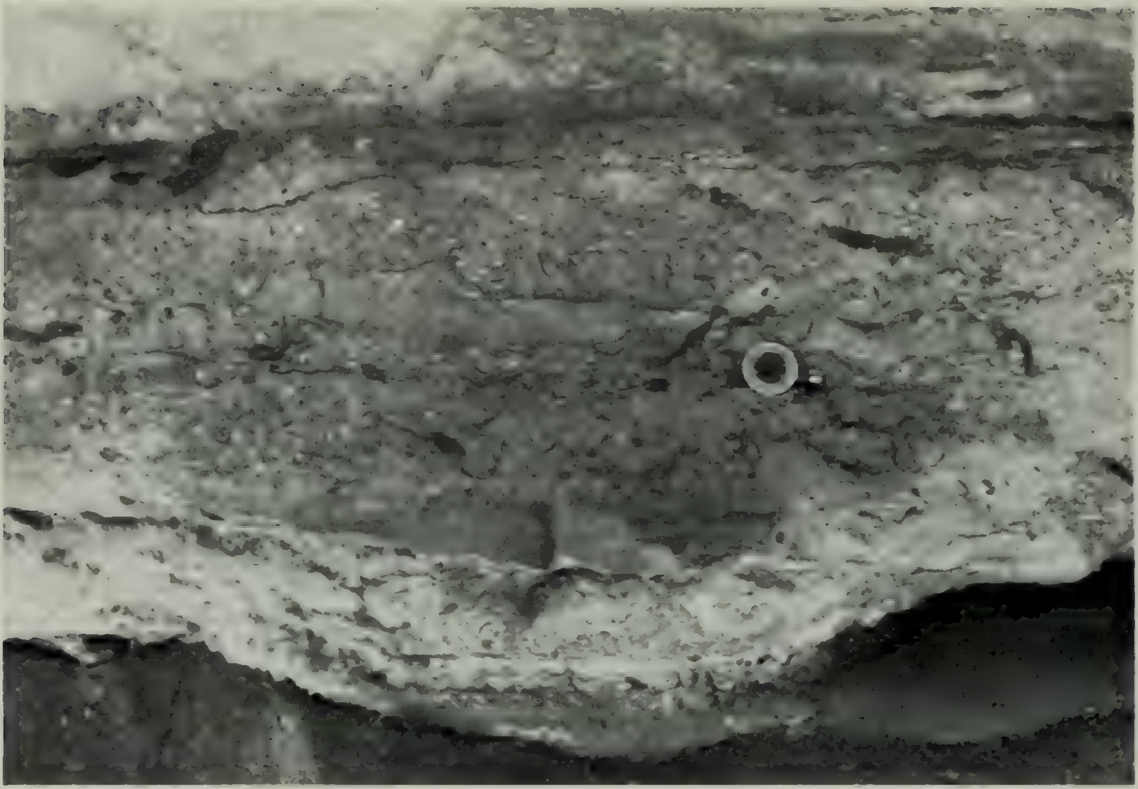

Fig. 5. Shelly limestone on granite platform, Elandspunt.

stone rests on a granite platform, thin-sections show a total absence of felspar grains. This is characteristic of a high-energy beach environment. The base of the coquina behind the Sea Harvest factory is in part phosphate mineralized by phosphate-rich solutions derived from the Miocene phosphorite at the Bomgat on the other side of the Hoedjiespunt peninsula. Even at the Bomgat the lower part of the Early Pleistocene limestone shows phosphate mineralization.

Wave-generated granite boulders occur at the base of the coquina at Elandspunt. The coquina consists of much disarticulated and fragmented bivalve fragments, and less fragmented gastropod remains. The coquina, shown in Figure 5, is very different from Late Pleistocene deposits (Fig. 11).

The Early Pleistocene mollusc fauna is shown in Table 1. The nature of the outcrop prevented a shell count being made at the Bomgat and Elandspunt sites. The fauna as a whole is indicative of shallow-water, mainly intertidal, conditions. Although *Bullia annulata* is commonly dredged today, it is sometimes found intertidally. All of the species of *Patella* are intertidal, except *P. tabularis* which is infratidal. *Littorina knysnaensis* is found most abundantly above HWS (high water spring). The barnacle *Balanus amphitrite*, which still encrusts the limestone bedrock at the Langebaan site, is usually indicative of the infratidal zone.

The Hoedjiespunt molluscs indicate, in general, the close proximity of a rocky shore. But whereas the Bomgat assemblage is characterized by abundant

TABLE 1
Early Pleistocene Invertebrate Fauna

	Bomgat	*Sea Harvest* %	*Elands-punt*	*Langebaan* %
GASTROPODA				
Haliotis midae Linnaeus		< 1		< 1
Fissurella robusta (Haughton)	×	30	×	2
Helcion cf. pruinosus (Krauss)	×	3		
Patella argenvillei Krauss		2		
P. barbara Linnaeus	×	7		2
P. cochlear Born		2		
P. granatina Linnaeus	×			
P. granularis Linnaeus		1		
P. oculus Born		< 1		
P. tabularis Krauss		< 1		
P. variabilis Krauss		< 1		
Gibbula rosea (Gmelin)				< 1
Turbo cidaris Gmelin	×	19		2
Oxystele trigina (Chemnitz)	×	< 1		
Littorina knysnaensis Philippi				1
'*Rissoa*' *capensis* Sowerby		×		
Solariella undata Sowerby				< 1
Cerithidea bifurcata Kilburn & Tankard				7
Crepidula sp.	×	18	×	26
Thais cingulata (Linnaeus)	×			
Purpura praecingulata (Haughton)				< 1
Burnupena papyracea cincta (Röding)	×	2		3
Triumphis dilemma Kilburn & Tankard			×	1
Bullia annulata (Lamarck)				3
B. digitalis Meuschen				4
B. laevissima (Gmelin)				1
Nassarius capensis (Dunker)				1
N. scopularcus Barnard				2
N. speciosus Adams				11
Fusus sp.				< 1
Peristernia nassatula (Lamarck)				1
Marginella capensis Krauss				< 1
Marginella piperata Hinds				2
Marginella sp.				< 1
Cythara amplexa (Gould)				< 1
Conus mozambicus mozambicus Hwass				1
BIVALVIA				
Aulacomya ater (Molina)		< 1		2
Perna perna (Linnaeus)	×	3		2
Gryphaea sp.		< 1		
Ostrea atherstonei Newton				< 1
Mysella convexa (Gould)				1
Tellimya trigona Barnard				1
Carditella capensis Smith				< 1
Thecalia concamerata Bruguière		< 1		< 1
Eucrassatella sp.				< 1
Lutraria lutraria (Linnaeus)				2
Tivela tomlini Haughton		1		< 1
Petricola prava Kilburn & Tankard		8		14
CIRRIPEDIA				
Balanus amphitrite Darwin		< 1		4
Total individuals	—	172	—	220

(× = present but not counted.)

Perna perna, the Sea Harvest assemblage has fewer bivalves and abounds in patellids. Although rock-dwelling forms are common at the Langebaan site, *Patella* is generally absent. Sand-dwelling forms predominate there. Furthermore, species such as *Cerithidea bifurcata* and *Thecalia concamerata* are indicative of sheltered mud flats.

Assigning these deposits to any age with confidence is difficult. Parker (1968) reports two ^{14}C dates for the Elandspunt site: 41 100 B.P. (Pta—097), and greater than 49 500 B.P. (Pta—098). Besides the fact that the ^{14}C technique is unreliable on carbonate of this age, there is also a distinct possibility that the molluscs were not collected *in situ* from the limestone. The number of extinct molluscs in the fauna seems to preclude a very young age. These include *Fissurella robusta*, *Cerithidea bifurcata*, *Crepidula* sp., *Purpura praecingulata*, *Triumphis dilemma*, *Tivela tomlini*, and *Petricola prava*. The *Crepidula* possibly originated from a *C. porcellana*-type ancestor (Kilburn & Tankard 1975). Stratigraphically the fauna resembles the 45–50 m transgression complex fauna of the Namaqualand coast. It has in common *Fissurella robusta*, *Purpura praecingulata*, *Triumphis dilemma*, the large form (20 cm) of *Perna perna*, and *Petricola prava*. The absence of *Donax haughtoni* and *Striostrea margaritacea*, 45–50 m transgression complex zone fossils, is attributed to the higher energy environment and colder water conditions in the Saldanha area.

Carrington & Kensley (1969) have assigned an Early Pleistocene age to the Namaqualand 45–50 m transgression complex. This is based on altimetric correlation with the Moroccan succession, the number of extinct species, the low degree of lithification, and the fresh appearance of the shells. They also note that this was the last warm water fauna. Assuming that they are correct in assigning these deposits to the Early Pleistocene, the rate of tilting, already discussed, agrees well with Dingle's (1973*b*) estimate.

THE 13 m SHORELINE

At the southern entrance of the Elandsberg tunnel at Cape Deseada there is a prominent horizon of large wave-generated boulders banked against the foot of the cliff at 13 m a.s.l. Another horizon of well-rounded cobbles and boulders occurs beneath talus material on the southern shore of Verlorevlei at 13 m a.s.l. No fossils are associated with these two horizons. This shoreline is pre-Late Pleistocene since it is considerably higher than the Late Pleistocene sea level datum. Possibly it correlates with the 10 m Early Pleistocene deposits of the Saldanha area. If younger than that, then the most likely correlation would be with the Namaqualand 17–21 m transgression complex which Carrington & Kensley (1969) assign to the Middle Pleistocene.

LATE PLEISTOCENE MARINE HISTORY

The geomorphology and mollusc fossils indicate several depositional environments. An open-coast facies includes rocky shores and exposed sandy shores. An estuarine-lagoonal facies is identified in the vicinity of Saldanha Bay–Langebaan Lagoon, Berg River, and Verlorevlei. At Velddrif (Figs 1, 10) lagoonal deposits are situated between breaker-bars of the open-coast facies. The mollusc fauna of the open-coast facies includes rock and sand-dwelling forms which still inhabit the adjacent coast. But the estuarine-lagoonal facies regularly contains several species which today live in tropical waters to the north.

Description of the marine deposits between Ysterfontein and Elands Bay will be discussed according to the dominant depositional environment which also coincides closely with a regional approach. The mollusc fauna has been described elsewhere (Tankard 1975).

Open-coast facies

Rocky shores

Formation of a platform results from waves breaking in shallow water and the movement of detritus across the rock surface. All bottom loss of energy takes place shoreward of the surf base, which Dietz (1963) defines as the greatest depth where the waves begin to peak appreciably during storms. The depth of vigorous abrasion is thus 1,5 times the wave height. The abrasion platform is a function of the energy generated by the average waves. The depth of the abrasion base off the Cape Peninsula is 15 m (B. W. Flemming in press). Wave energy is reflected from slopes greater than 30° so that erosion is slow, while maximum erosion takes place on slopes less than 15° (N. C. Flemming 1965). Examples of this are, firstly, the Chapmans Peak coast of the Cape Peninsula where a very steep slope and consequent reflection of wave energy is associated with little erosion. Secondly, in the Saldanha area slopes are low and vigorous abrasion has resulted in a well-defined platform.

In the Saldanha area mean wave height is 3 m (Pomeroy 1965), suggesting that most vigorous abrasion will take place shallower than 4,5 m. Davies (1973) attempts to identify Holocene platforms which are related to sea levels at 5,4 m, 3,9 m, and 1,8 m a.s.l. The platform on the seaward side of the Vredenburg pluton varies in altitude up to 10,7 m (Visser & Schoch 1973), so that the relief is about 7 m. It is likely that the platform was eroded during a single stationary sea level. It is highly unlikely that short-term oscillations of sea level would have left a permanent record on a platform of low relief.

Table Mountain sandstone forms a natural groyne at Cape Deseada where structually controlled abrasion has formed a narrow platform. The outer margin of the platform is 4,7 m a.s.l., and the inner margin 6,5 m a.s.l.

The most widespread platform is that bordering the Vredenburg pluton, broken only by the deep entrance to Saldanha Bay. At Hoedjiespunt bedded Miocene phosphorite lies in a bedrock depression with a contact at 5,25 m a.s.l. This suggests that the platform may be an old feature that originated in the Miocene. Tankard & Schweitzer (1974) have shown that a similar planation surface at 7–8 m a.s.l. at Die Kelders on the southern Cape coast is overlain by Neogene limestone. But Early Pleistocene limestones in the Saldanha area suggest that there the platform has been remodelled in the Pleistocene, and that it is a composite feature. 'Fresh' stacks on the North Head platform possibly originated in the Late Pleistocene. The present sea does not appear to be cutting a notch or platform at mean sea level. Instead the rocky shore plunges vertically about 3–4 m before flattening out on to a sandy bottom.

Parker (1968) has mentioned two beach ramparts which parallel the present coast on the North Head and South Head platforms. Both ramparts, or storm beaches, are composed of well-rounded granite boulders with a matrix of coarse sand and comminuted shell. Slight imbrication of the boulders suggests that storm waves have played little part in forming these ridges. The outer rampart on North Head is a composite feature. It rises from the shoreline with a concave surface to a vegetated crest 7 m a.s.l. It thus has a fossil as well as a modern component. The second rampart (Fig. 6) peaks at 12,1 m a.s.l., and is approximately 40–50 m behind the lower and outer rampart. The flat between them is underlain by coquina and shelly sand typical of an upper foreshore accretionary unit. It abuts against the inner rampart. Pans have developed behind the ramparts.

The crests of these ramparts, like breaker-bars, probably relate to MHWS, which at St. Helena Bay is 0,75 m above MSL. The two ramparts thus reflect

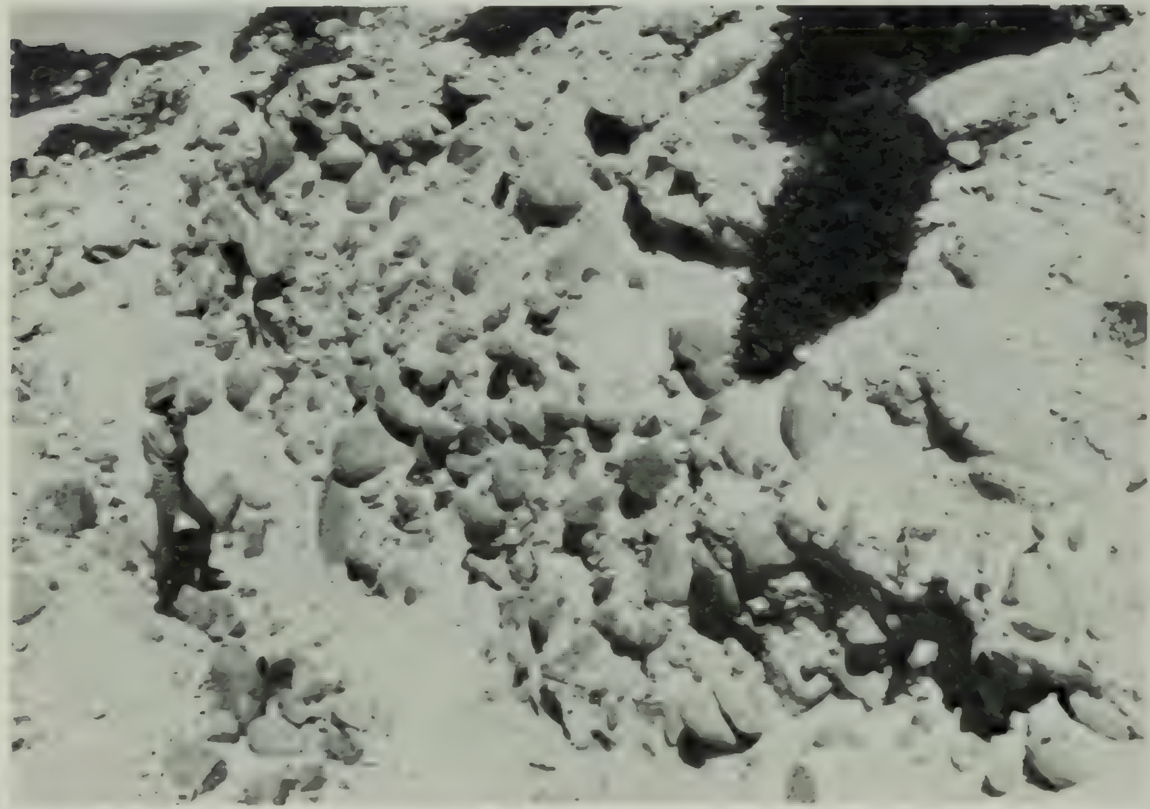

Fig. 6. Excavation through inner storm beach on North Head platform. Elevation of the crest is 12 m a.s.l.

sea levels at 6,25 m and 11,35 m a.s.l. The 7 m rampart would most likely be of last interglacial age since it agrees with the Late Pleistocene datum, but the 12 m rampart would be older, and of unknown age.

Shell deposits are extensive on the platform and Tankard (1975, table 1) has tabulated the mollusc assemblages at two sites, namely Paternoster and North Head. Parker (1968) has listed the molluscs from other sites. A horizontally bedded shelly sand is exposed below the Paternoster lighthouse. The bedding takes the form of layers of complete shells separated by layers of comminuted shell. Whole shells constitute 25–30 per cent of the organic remains. Gastropods constitute 96 per cent of the assemblage. Most species are rock-dwelling intertidal forms. Only *Patella compressa* of the six patellids is infratidal (Branch 1971). *Conus scitulus* and *Cypraea algoensis* are common.

The Paternoster deposits are typical of the marine sediments covering the platform. Rock-dwelling forms are always in excess of 90 per cent, and gastropods predominate. On the North Head platform at the entrance to Saldanha Bay occasional (< 1 %) and stunted *Ostrea atherstonei* valves occur. There are also seal bones. Barnacles are common. Due to maximum exposure to the swell this part of the platform has a great amount of comminuted shell (> 95 %). Beach rounded boulders and cobbles are common, as well as fragments of coquina.

These shell beds regularly occur up to 6 m a.s.l. This and the outer rampart suggest a Late Pleistocene shoreline dominated by a 6,25 m sea level.

Several localities have features which suggest lower sea levels than that at 6,25 m a.s.l. There is an intertidal occurrence of beachrock at the northern end of Jutbaai. It is a medium-grained skeletal lime grainstone. The lath-shaped, well-rounded shell detritus constitutes 95 per cent of the rock. The absence of felspar is characteristic of a beach environment. The shell and echinoid spine detritus shows a preferred orientation, and is drusy calcite cemented. Coquina is preserved at two further localities amongst beach boulders at 1,6 m a.s.l. and 3,9 m a.s.l.

An horizon of bedded wave-generated boulders is situated within the Bomgat at 3,5 m a.s.l. The Bomgat is an extension of a gully through the granite platform through which waves surge high above mean sea level. The cave deposit was probably formed above high tide level and would have been related to a sea level between present datum and 2 m a.s.l. A single ^{14}C date (3 500 B.P.: Mr B. Flemming, pers. comm.) derived from mollusc shell collected *in situ* from the boulder beach horizon suggests that this feature probably dates to the Holocene.

Exposed sandy shores

Waves tend to break further from the shore with decreasing gradient so that there is also a decreasing amount of energy available for shoreline erosion (N. C. Flemming 1965). With loss of energy in crossing the shallow floor, coarse stirred-up particles are deposited and these lead to formation of breaker-bars (Holmes 1965). Since the slope of the sea floor adjacent to the Berg River is only 1 in 400, one would expect accretion units to develop. But this area is relatively sediment-starved since perennial runoff is restricted to the Berg River, which contributes only a small quantity of sediment, and the Cape submarine canyon possibly acts as a sediment drain.

Late Pleistocene sandy shore deposits are most prominent between Slippers Bay (west of Berg River mouth) and Cape Deseada. The present shoreline forms a smooth curve. At Cape Deseada, where the coastal plain is narrowest, aeolian sands tend to form a concave profile. Further south the coastal plain becomes more complex.

1. *Evaporite deposits*

Gypsum deposits are frequently encountered on the flats behind the coastal dunes (Fig. 1). Generally, these evaporite deposits are less than 6 m in altitude and are believed to be mainly of last interglacial age. The evaporite deposits north of Dwarskersbos (Fig. 1, Gyp 2) and Ysterfontein (Gyp 7) are probably still forming today since they are associated with salinas. (A salina is a modern salt pan on an arid coast.) Visser and Schoch (1973) record several $CaSO_4.2H_2O$ determinations on these deposits. The gypsum content of the evaporite deposits usually exceeds 80 per cent. The gypsum usually occurs in uneven masses of fine-grained texture. Elevations above sea level are as follows: Cape Deseada (Gyp 1) 4,5–5 m; north of Dwarskersbos (Gyp 2) 3,5–4,5 m; Kruispad (Gyp 3) 3,5 m; St. Helena Bay area (Gyp 4 & 5) 3 m; Naval Academy (Gyp 6) 2 m; Ysterfontein (Gyp 7) 2 m.

The Cape Deseada occurrence (Gyp 1) was the only one examined in detail. Here the coastal plain is backed by 180 m high sandstone cliffs. The sedimentary succession of the terrace from bottom to top is as follows:

(i) shelly calcareous sands overlying the sandstone platform;
(ii) rhythmically laminated (2 mm units) carbonate-gypsum-halite units (Fig. 7);
(iii) a thin layer of saline mud;
(iv) modern dune sands which also form extensive coastal dunes.

The shelly calcareous quartzose sands at the base are attributed to a transgression to 6–7 m a.s.l. The mollusc assemblage is indicative of an intertidal sandy beach, except for *Choromytilus* which is a rock-dweller. *Solen capensis* suggests a sheltered environment which, adjacent to the present high energy beach, could only have prevailed in a lagoonal environment on the leeward side of a breaker-bar. An extensive emerged bar which once formed a barrier-beach follows the St. Helena Bay coastline. In the Cape Deseada region a salina must have developed behind the bar. Flooding of the salina would have occurred at spring tides. Precipitation from the stranded brine led to formation of the evaporite. The evaporite is now about 0,75 m thick and would have

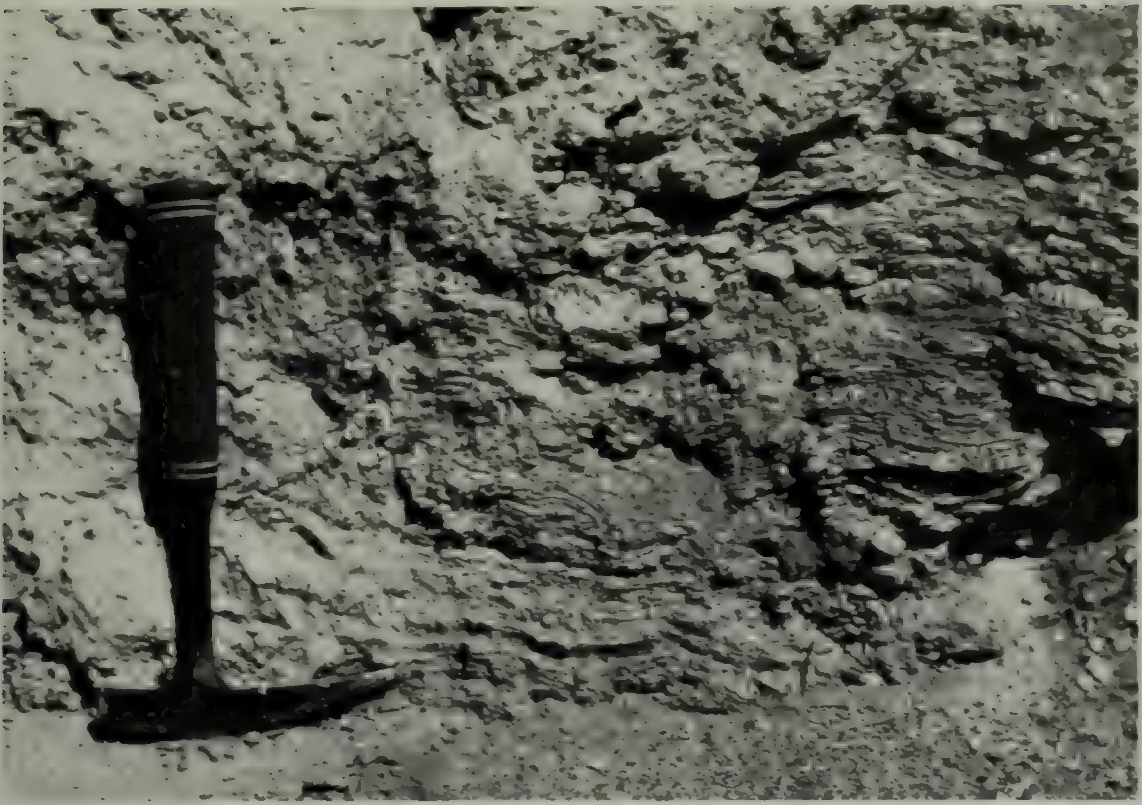

Fig. 7. Cape Deseada evaporite deposit.

required a sea-water column of 45 m for its formation (by extrapolation from statistics quoted by Hsü 1972).

The evaporite contains a microfauna suggestive of a complex history of formation. The microfauna is summarized in Figure 8 and Table 2. The foraminifers, which constitute only 5 per cent of the assemblage, are all abraded. In contrast, the ostracodes (95 per cent of the assemblage) are thin-shelled, show no signs of abrasion, and are frequently still articulated. All growth stages are also encountered. *Candona* sp., *Pionocypris assimilis*, and *Cypridopsis ochracea* are all freshwater species. *Aurila dayii* suggests a more saline environment as found in estuaries and lagoons. *Cyprideis* cf. *limbocostata* is an inhabitant of brackish water, salt lagoons and marsh environments. Species of *Cyprideis* have both smooth forms and nodose forms, but the number of nodose dimorphs decreases with decreasing salinity (Benson 1961). The smooth tests of *Cyprideis* cf. *limbocostata* confirms the freshwater nature of the assemblage.

Since freshwater ostracodes are scarce in waters more saline than 2‰ (Benson 1961), the Cape Deseada assemblage must reflect low salinities considering the abundance of these ostracodes. But gypsum will only precipitate from a brine at salinity of about 117‰, 3,35 times that of normal sea-water. The apparent contradiction between the ostracode evidence and the gypsum evidence suggests a complex history of sea-water inflow, evaporation to dryness, and freshwater inflow (Fig. 9).

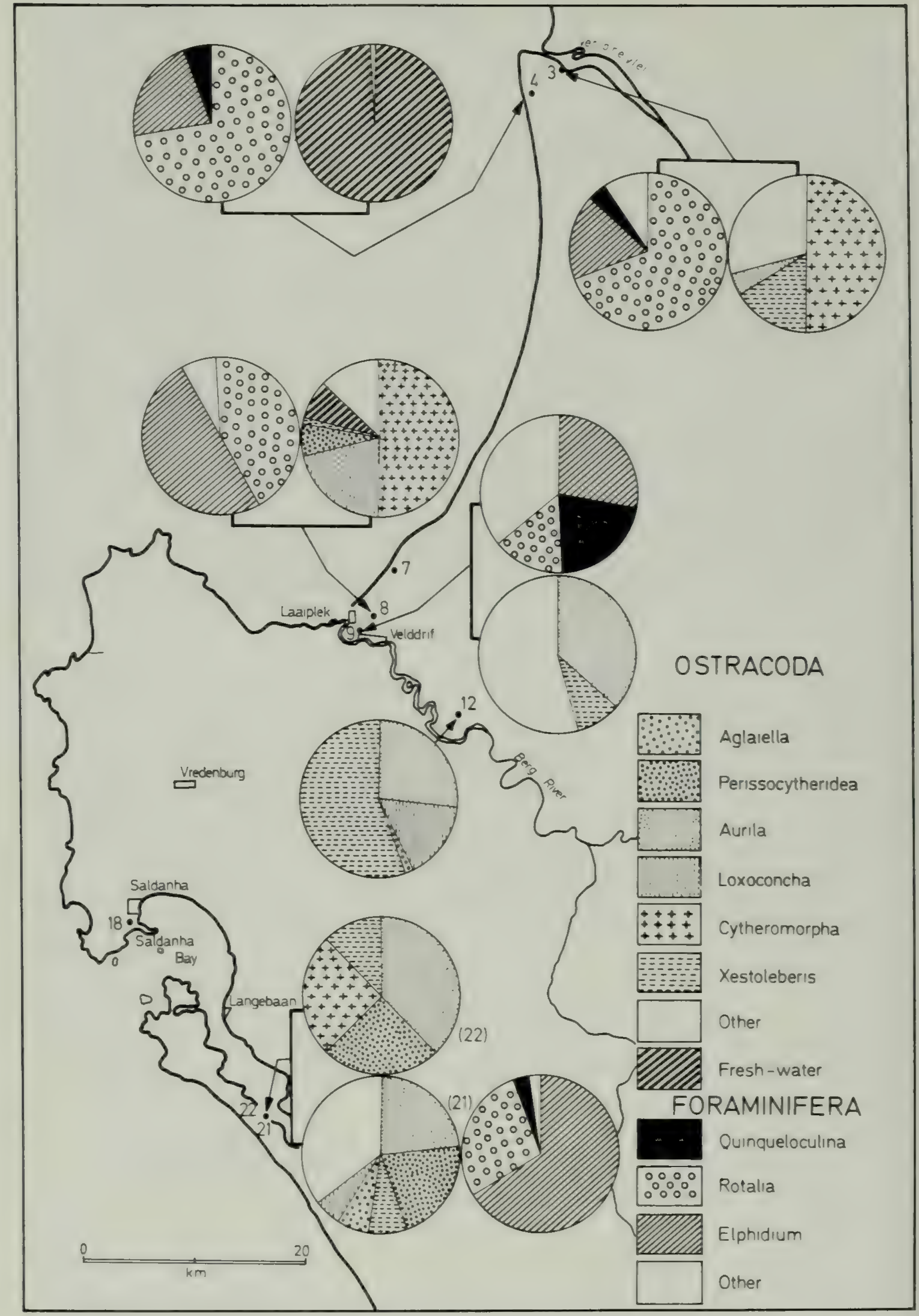

Fig. 8. Distribution of ostracode and foraminifer faunas.

TABLE 2

Late Pleistocene Microfauna

FORAMINIFERA *Sites*	3	4	7	8	9	12	18	21	22
Quinqueloculina spp.	3	6			21		×	×	×
Sigmoilina sp.									×
Frondicularia sp.	< 1								
Lagena hexagona (Williamson)	< 1				3	×		×	
Lagena semistriata Williamson	7			3					
Lagena cf. orbignyana (Seguenza)				< 1					
Lagena spp.					2	×	×		
Bolivina variabilis (Williamson)	< 1				23				
Bulimina sp.					7				
Rotalia beccarii (Linnaeus)	69	73	×	46	15	×	×	×	
Elphidium alvarezianum (d'Orbigny)	17				6				
Elphidium macellum (Fichtel & Moll)	1		×		21				
Elphidium spp.		21		50		×	×	×	
Cibicides cf. pseudoungeriana (Cushman)	< 1								×
Cibicides spp.						×			
Virgulina cf. advena Cushman					2				
OSTRACODA									
Eucypris sp.				1					
Paracypretta ampullacea Sars				7					
Cypridopsis ochracea Sars		69							
Pionocypris assimilis Sars		25							
Candona sp.		2							
Paracypris westfordensis Benson & Maddocks				5					
Aglaiella railbridgensis Benson & Maddocks						1		7	
Cytheretta knysnaensis Benson & Maddocks					×				
Cyprideis cf. limbocostata Hartmann		2							
Perissocytheridea estuaria Benson & Maddocks				6				6	
Cytherura sp.				< 1					
Hemicytherura parvifossata Hartmann					×				
Bairdia cf. villosa Brady								1	
Aurila dayii Benson & Maddocks	4	1			×	27		22	38
Caudites knysnaensis Hartmann					×				
Procythereis sp.								4	
Urocythereis sp.		1		< 1				12	
Loxoconcha parameridionalis Benson & Maddocks	< 1			< 1			×	20	25
L. peterseni Hartmann				21		16		3	
Cytheromorpha sp.	49			49				7	25
Bradleya sp.	8			7				10	
Xestoleberis capensis G. W. Müller	17			1	×	56	×	8	12
Cytherella punctata Brady	21			< 1					

(Values expressed as percentages separately for Ostracoda and Foraminifera. × = present but not counted.)

Krumbein & Sloss (1963) discuss the origins and associations of evaporite deposits. Two conditions are necessary for the genesis of evaporites: a warm and arid climate with little freshwater run-off, and a restricted body of seawater. Excessive evaporation at high temperature and little dilution by inflow of freshwater raises salinity above that of the open sea, and ultimately leads to precipitation of salt. Calcium carbonate is the first to precipitate when

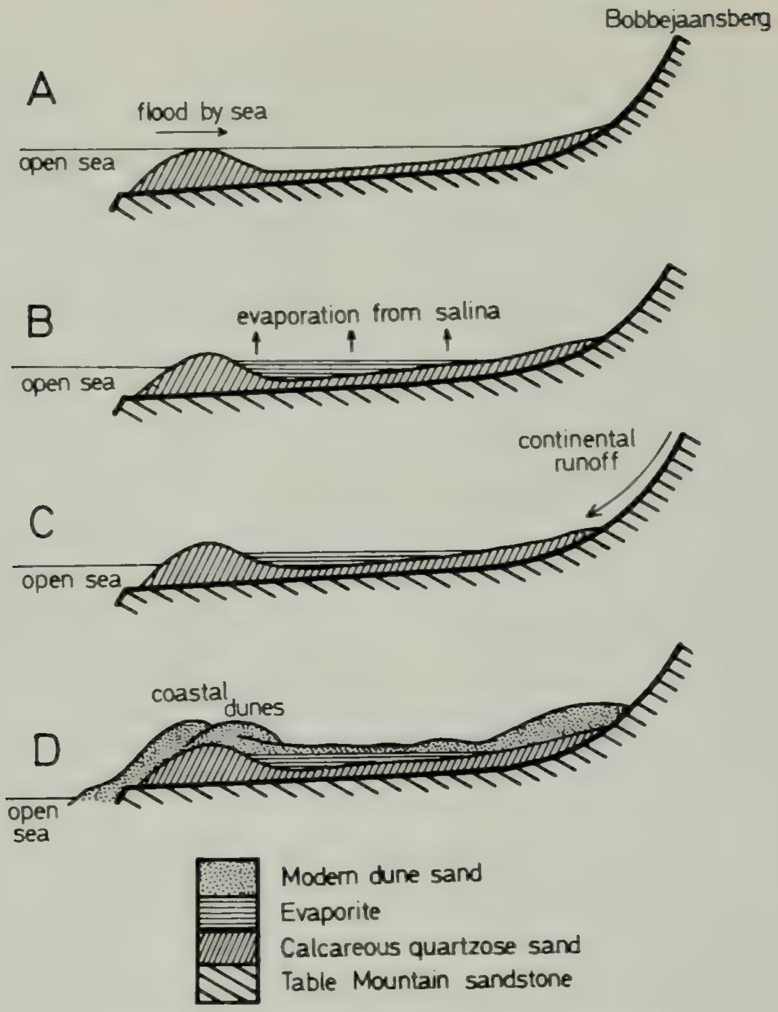

Fig. 9. Summary of the history of evaporite accumulation at Cape Deseada.

evaporation halves the volume of water. Gypsum is next to precipitate at about 25 °C, followed by halite after 85 per cent of the gypsum has precipitated.

At Cape Deseada a restricted lagoon has developed behind an emerged breaker-bar in a warm and arid climate. The mollusc fauna of this transgression suggests a hydroclimate warmer than today (Tankard 1975). Present-day rainfall is less than 200 mm/year. Microscopic examination of evaporite specimens shows that each cycle begins with carbonate precipitation, and is followed by gypsum and frequently by halite. But the absence of halite in some of the units suggests inflow of more sea-water, probably tidal, before precipitation of gypsum from the previous brine had been completed. The precipitation cycle would be terminated at that stage and a new cycle initiated. Since each carbonate-gypsum-halite unit is, on average, about 2 mm thick, it would have taken 300 to 400 tidal floodings of the salina (Fig. 9, A–B) to accumulate the 0,75 m of evaporite. The broken foraminifer tests suggest that they have come from the neighbouring high-energy beaches. Complete evaporation of the brine was occasionally followed by inflow of freshwater, runoff from the sandstone hills, to produce freshwater pans (Fig. 9, C). This is suggested by the ostracode fauna of freshwater affinity (salinity less than 2‰). The articulated valves and completeness of the thin-shelled carapaces suggest little agitation and the abundance of juvenile forms suggests that the population was probably suddenly exterminated, possibly by another tidal flooding of sea-water.

It is possible that the unique conditions of a saline water–freshwater cycle could also be satisfied by movement of sea-water through the shelly breaker-bar, rather than over the top during high tides as suggested above. The sea-water would at some stage meet and dip beneath ground-water (density control). Saline or freshwater conditions in the salina area would then depend entirely upon advance or retreat of the mixing zone due to ground-water fluctuation.

2. *Barrier-beach coast*

The entire length of St. Helena Bay coastline is marked by an emerged breaker-bar which, at some stage, must have formed a barrier-beach. Dune sands now accentuate the crest of this breaker-bar. But only south of Dwarskersbos are there any good exposures.

North-east of Dwarskersbos (2,5 km) surface exposures show the terrace behind the bar to consist of shell beds with entire valves in a predominantly detrital shell deposit with pebbles of Malmesbury rock. The shells are not evenly distributed throughout the exposure. Frequently shells of one species, e.g. *Aulacomya ater*, may occur together. The mollusc assemblage is characteristic of an intertidal sandy shore.

The assemblage is dominated by *Crepidula capensis* (46,7 %), *Tellina trilatera* (12 %), and *Venerupis senegalensis* (12 %). The predominance of undamaged valves of *T. trilatera*, a thin-shelled species, suggests relatively low energy conditions such as are presently found on the adjacent shore.

5,5 km south-west of this site the mollusc assemblage is very different. *Crepidula capensis* is less dominant, *Tellina trilatera* is totally absent, and *Lutraria lutraria* and *Argobuccinum argus* make up nearly 70 per cent of the assemblage. Many barnacles, patellids, and *Choromytilus meridionalis* suggest a partly rocky shoreline. There are also many angular Malmesbury rock fragments. The Malmesbury platform is at 4 m a.s.l.

The Malmesbury platform continues west of the Berg River, and is exposed behind the Varkvlei homestead where it is associated with rounded boulders at 6,7–7 m a.s.l. (Visser & Schoch 1973). A deep excavation west of the homestead penetrated 4 m of horizontally bedded shell deposits with little detrital quartz before reaching the Malmesbury platform at 1 m a.s.l. The platform was mantled with wave-generated boulders. The shell bed rises gently inland to an elevation of 6 m a.s.l.

Two breaker-bars are well developed in the Velddrif area (Fig. 10). They are composed mainly of shell material with little detrital quartz, suggesting low sedimentation rates. Longitudinal excavations show subhorizontal bedding with alternating beds of whole shells and fragmented shells.

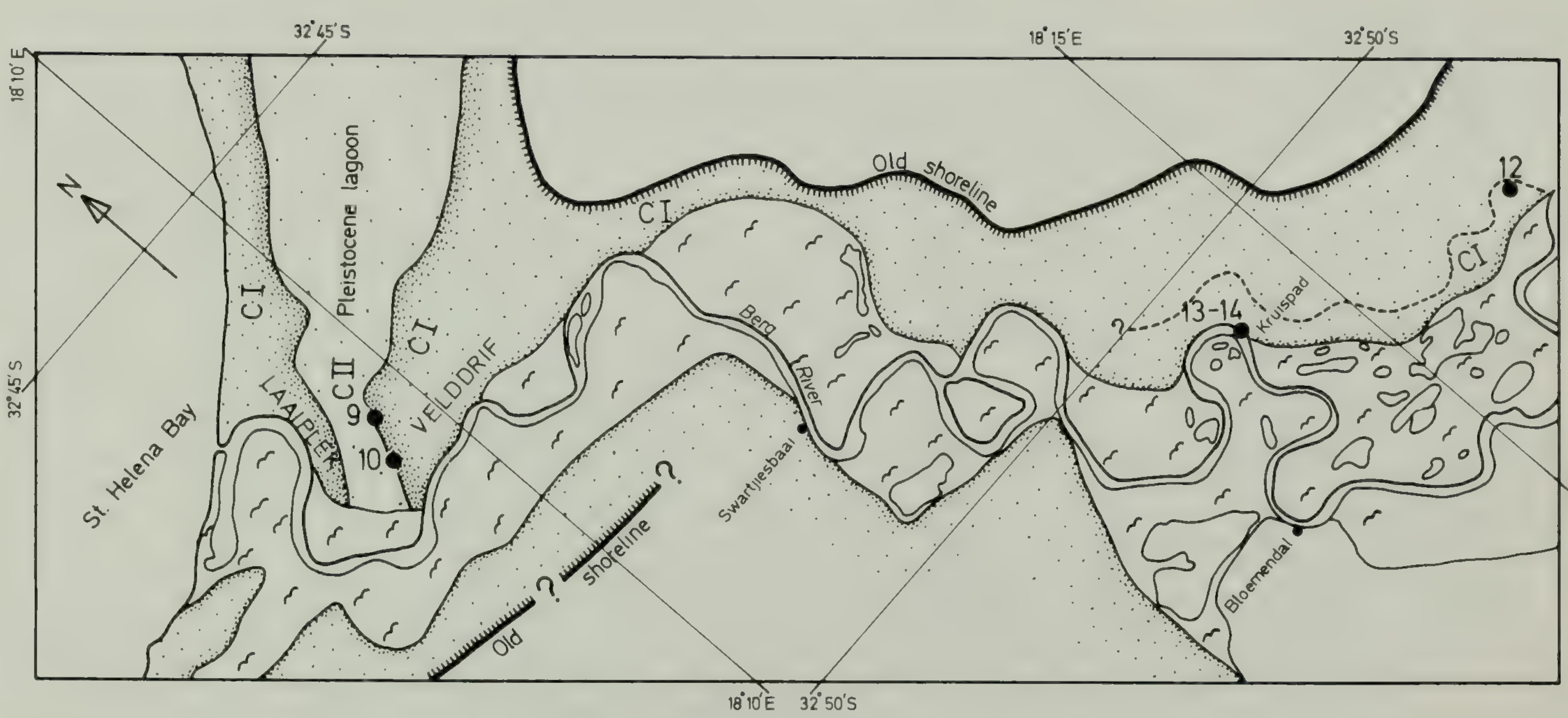

Fig. 10. Late Pleistocene marine features in the Velddrif area. Note the two bars which parallel the present coast. Broken line on Kruispad indicates furthest inland extent of shell beds.

The mollusc assemblage of the outer bar north of Laaiplek is dominated by *Crepidula capensis*, and *Venerupis senegalensis*. The top 0,5 m of the bar has a maximum of whole shells, and *Venerupis senegalensis* has a high articulation ratio (6,2). This horizon is underlain by 1,1 m of comminuted shell. *Scissodesma spengleri* is common. Its present geographic range is False Bay to Algoa Bay (Barnard 1964), suggesting slightly warmer conditions in the Late Pleistocene. The assemblage suggests an intertidal sandy beach. Figure 11 shows the concentration of shell debris and articulated shells constituting the bar.

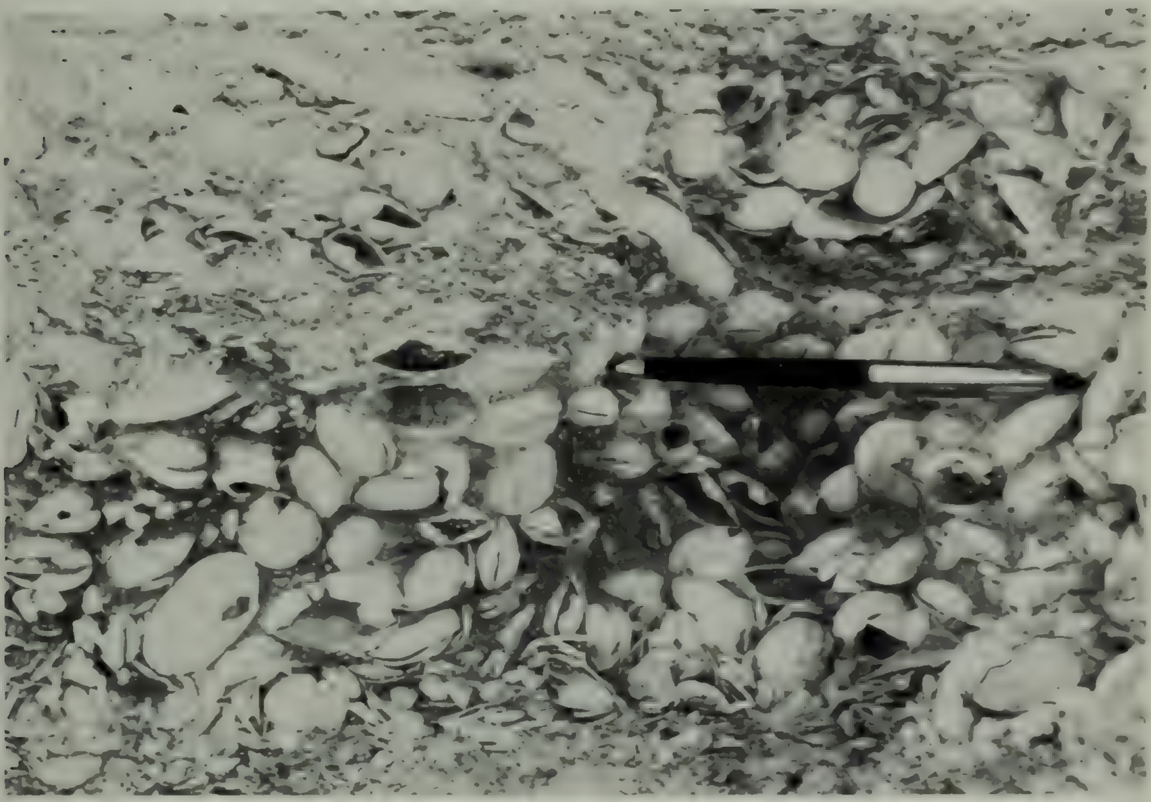

Fig. 11. Shell accumulation typical of the bar deposits (north of Laaiplek).

The seaward side of the second bar at Velddrif (site 9) is constructed of four basic units (Figs. 12–13). The lowest unit is at least 0,5 m thick (base concealed) and consists of horizontally bedded sand and shell debris. From 2,5 m a.s.l. to 3,6 m a.s.l. whole bivalves increase in proportion. The disarticulated valves are convex-up and have a preferred long-axis direction 220°. Then follows 1,4 m of fine quartzose sand with several shell bands containing articulated *Perna perna*. Other bivalves are convex-up and have a preferred long-axis orientation 130°. The fourth unit from 5 m–7 m a.s.l., consists of a cross-bedded, partially cemented shell deposit, with cross-bed azimuths 180°–220°.

Wave-energy appears to have been at a maximum in the lower unit where shell debris is broken down and finer quartz sand winnowed out. Incipient bar

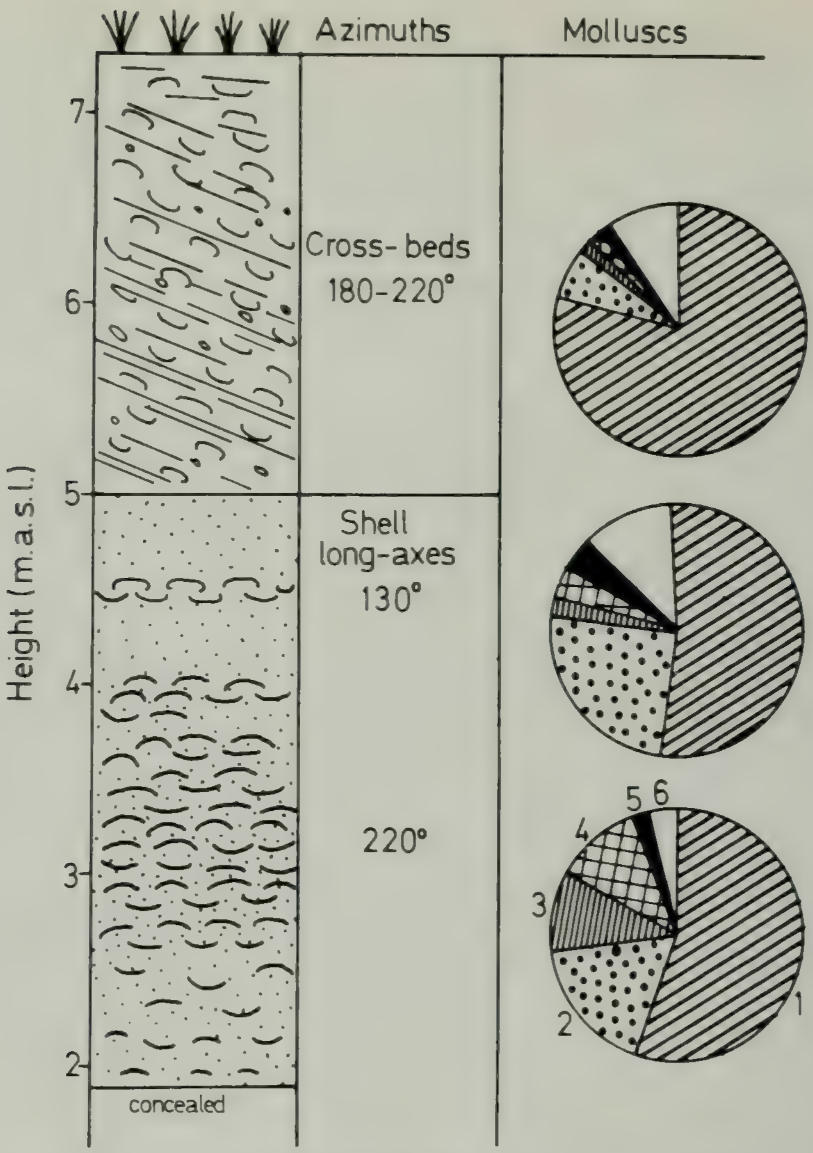

Fig. 12. Measured section through the inner bar and washover-fan at Velddrif. 1 = *Venerupis senegalensis;* 2 = *Crepidula capensis;* 3 = *Bullia laevissima;* 4 = *Lutraria lutraria;* 5 = *Perna perna;* 6 = Other.

development to the west reduced the wave-energy and resulted in a greater amount of unfragmented shell. But the very thick shells of *Venerupis senegalensis* reflect the high energy conditions near by. Further growth of the breaker-bar afforded a greater degree of shelter. Energy on the leeward side was insufficient to winnow away the fine quartz sand. Fragile *Perna perna* and *Phaxas pellucidus* lived in the sand. There are generally more juveniles in these sediments, and *Venerupis senegalensis* is thinner shelled. There was only enough energy to turn the shells over, but not enough energy to fragment them (Fig. 14). Finally, the bar migrated shoreward over the lower units. Cross-bedding frequently dips 10°, but dips in the uppermost part of the bar are shallow and characteristic of a washover fan.

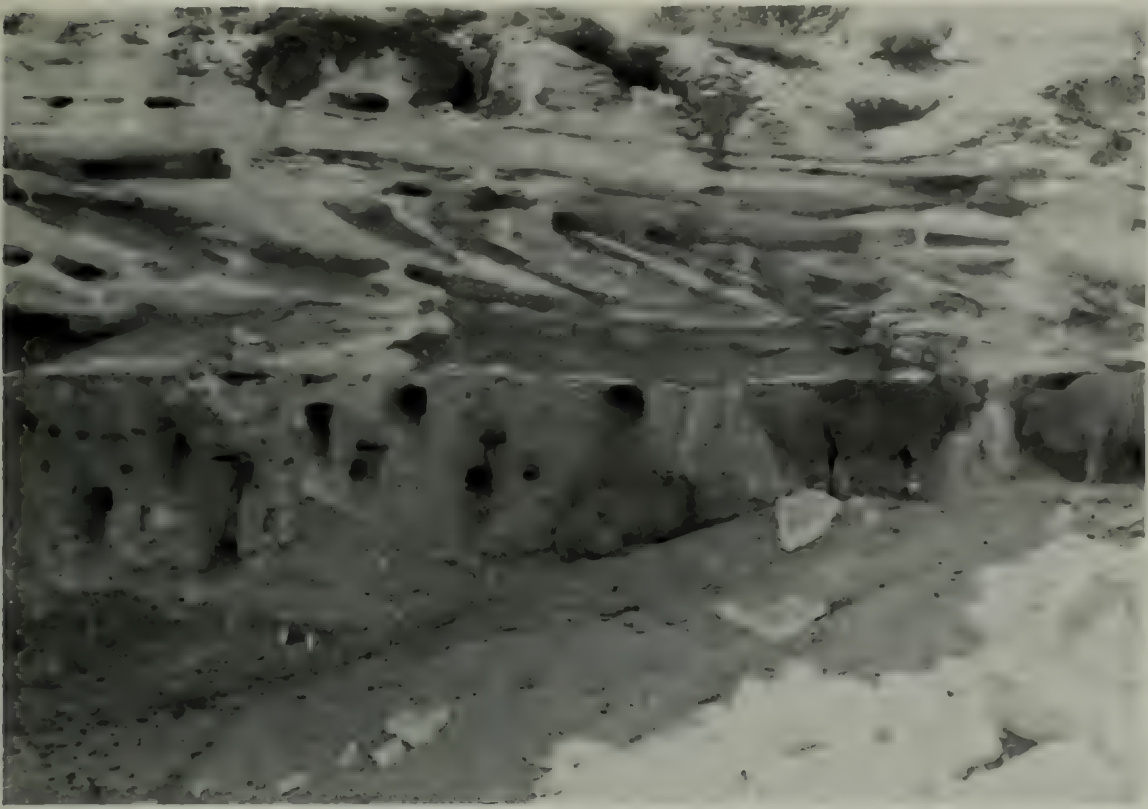

Fig. 13. Bar exposure at Velddrif.

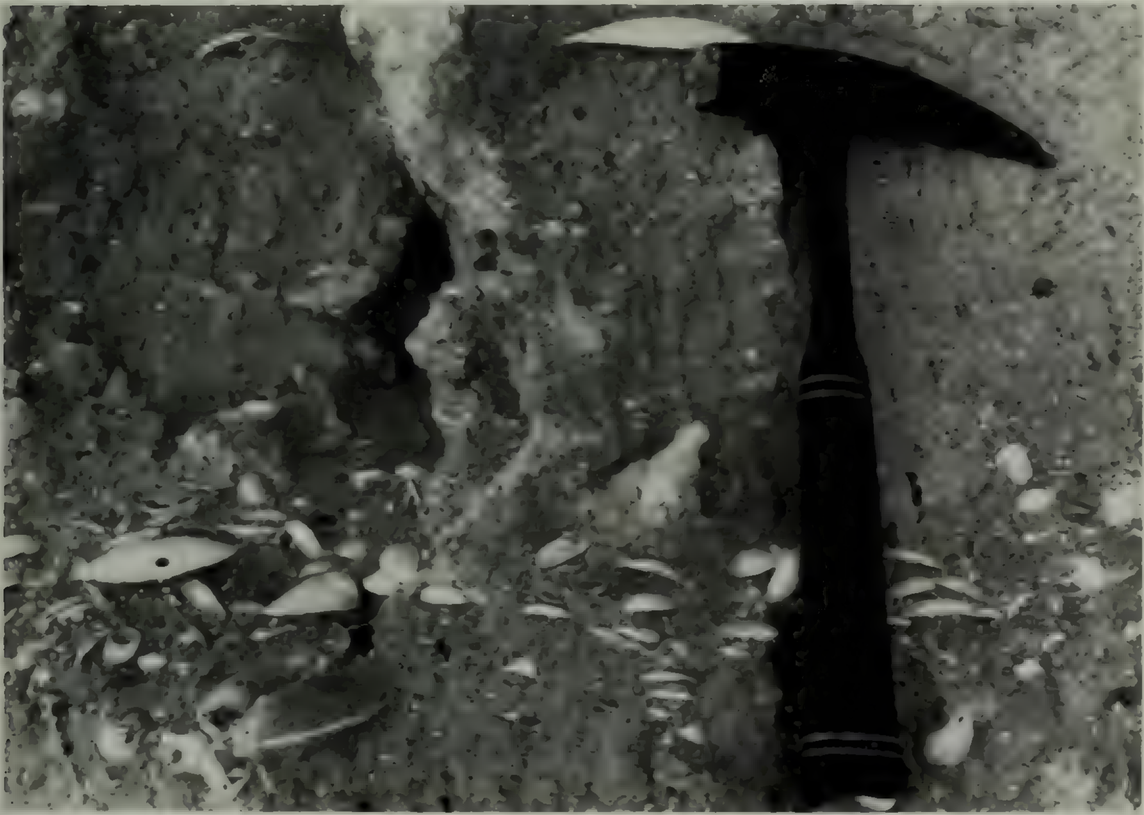

Fig. 14. Convex-up bivalves in the quartzose sand unit of the inner bar. Note articulated *Perna perna* (lower left) (Velddrif).

The fine quartz sand reflecting sheltered conditions was not necessarily brought across the top of the bar, but could have arisen from longitudinal transport on the leeward side and could have derived from tidal channels. Another excavation in the bar south of Velddrif shows small-scale cross-beds suggestive of a tidal inlet.

Figure 11 shows the typical composition of the mollusc assemblage. Sand-dwelling forms predominate, and of these *Venerupis senegalensis* always exceeds 50 per cent, and in the upper cross-bedded unit 81 per cent. Thin-shelled *Perna perna* are commonest in the sandy unit. There are also burrows in the sandy unit, possibly *Callianassa.*

The crest of the bar (7 m a.s.l.) is a washover fan which relates to MHWS and can be correlated to a last interglacial sea level of 6,25 m a.s.l.

Estuarine-lagoonal facies

Shorelines of the open-coast facies parallel the present shoreline very closely. Besides Saldanha Bay and its southerly offshoot Langebaan Lagoon, the Late Pleistocene sea extended up the Berg River valley and along Verlorevlei to form two extensive estuaries. Whereas the open-coast facies is continuous, the estuarine-lagoonal facies is discontinuous.

Verlorevlei

Verlorevlei is situated in a north-west trending drowned valley which was formed along a fault-plane by the ancestral Papkuils, Antonies, and Kruis Rivers which now feed into the head of the vlei. Fossiliferous sediments are exposed on the steeper southern bank. The present vlei is 16 km long, and a maximum of 1,5 km wide. The present mouth of the vlei is marked by a bar or platform of Table Mountain sandstone at 1 m a.s.l. A slight rise of sea level, as in the last interglacial, would effect considerable environmental changes, although the low bar at the mouth would still ensure a low energy regime. Recent bridge foundations showed that the deepest channel, and hence the original mouth, was further to the north.

Geological sheet 3118 C/3218 A shows a sand-covered terrace on the north bank to 60 m a.s.l. A thick sand cover buries any evidence that may indicate a marine origin.

Late Pleistocene fossiliferous deposits (sites 1–3 in Fig. 1) are typical of a salt-water estuarine environment. Maximum thickness (site 3) is 2,2 m where shelly sands lie unconformably upon Palaeozoic siltstones. The highest contact is at 5 m a.s.l. where *Ostrea stentina* was found still adhering to the rock. The lowest 0,5 m of the shelly sand consists of complete shells and valves, fragmented shell, and fine-grained quartzose sand. From 1,5 m to 2,35 m a.s.l. is a reworked horizon where the original deposit is diluted with coarse, iron-stained sand. From 2,35 m to 3,8 m a.s.l. the deposit consists of poorly sorted colluvium with scattered shell debris.

The mollusc assemblage (Tankard 1975, table 1) consists of an infaunal bivalve element and a minor epifaunal gastropod element. The assemblage is dominated by *Dosinia lupinus* (50%), and contains several thermophilic species such as *Tellina madagascariensis*, *Loripes liratula*, *Macoma tricostata*, *Venerupis dura*, etc. The assemblage suggests an estuarine sandy substrate. But *Argobuccinum argus*, *Burnupena papyracea*, *Oxystele variegata*, *Patella* spp., *Ostrea stentina* indicate that the shore was in part rocky. The low number of rock-dwelling forms shows that they were derived from a neighbouring environment which may not have been extensive.

The ratio of foraminifers to ostracodes (Fig. 8, Table 2) is 9 to 1, indicating an open exit to the sea. *Cytheromorpha* sp., which constitutes 49 per cent of the ostracode assemblage, can tolerate brackish water. *Aurila dayii*, *Loxoconcha parameridionalis*, *Xestoleberis capensis*, and *Cytherella punctata* are today found in estuarine environments (Benson & Maddocks 1964; Hartmann 1974). They indicate saline water and a sandy substrate. *Xestoleberis* and *Loxoconcha* indicate the presence of marine grasses such as *Zostera*. The Foraminifera are dominated by *Rotalia beccarii* (69%) and *Elphidium alvarezianum* (17%). *Rotalia beccarii* thrives in brackish water (Loeblich & Tappan 1964).

Estuarine animals generally colonize the area from mid-tide to low tide (Emery & Stevenson 1957). *Ostrea stentina*, which encrusts the rock at 5 m a.s.l. is always found infratidally. These deposits would thus indicate a mean sea level in the region of 6 m a.s.l. or more.

The molluscs constitute a mixed life and indigenous death assemblage. Although some winnowing of juveniles may have taken place, the organisms appear to have lived in one broad environment reflected in the sediments (Tankard 1975).

Berg River

The Berg River has not developed a net of tributaries over the sandveld where infiltration capacity is high. In its lower reaches it meanders and gives rise to the usual features associated with meandering streams, e.g. oxbow lakes, meander scrolls. The last interglacial climatic peak was probably associated with aridity so that the Berg River did not flow as strongly as today, and a last interglacial transgression to 6–7 m a.s.l. would have extended saline conditions far up the valley.

Fossiliferous deposits containing marine molluscs are encountered 15 km up the Berg River on the farm Kruispad (Fig. 10). The terrace contains evidence for still-stands of the sea at about 6 m a.s.l. and 3,5 m a.s.l. The furthest inland extent of the terrace (Fig. 10) has been drawn from aerial photographs. The inner edge of the terrace is covered with dune sand and calcrete so that it is impossible to evaluate the significance of this shoreline. Mr D. S. Melck of Kruispad has determined the furthest inland extent of the shell deposits (Fig. 10) by hand-augering.

A shallow excavation southeast of the homestead and 15 km from the

Berg River mouth, revealed a shell bed beneath 1 m of dune sand. The surface of the shell bed is 5,1 m a.s.l. The mollusc assemblage is typically estuarine, and contains several tropical west African species: *Nuculana bicuspidata*, *Loripes liratula*, *Leporimetis hanleyi*, *Venerupis dura*, and *Panopea glycymeris*. Mr S. Kannemeyer of the South African Museum identified the otolith of the sea eel *Tachysurus fossor*. Excavation shows *Panopea glycymeris* to be always articulated and in life orientation, and on the same plane 0,6–0,7 m from the surface of the shell deposit, i.e. a siphon-length from the surface. Living *Panopea glycymeris* in the Mediterranean is always infratidal, and never extends into the intertidal zone. This suggests a sea level in the vicinity of 6 m a.s.l. or higher.

The microfauna (Fig. 8, Table 2) consists almost entirely of ostracodes, and the dominant species are *Aurila dayii* (27 %), *Loxoconcha peterseni* (16 %), and *Xestoleberis capensis* (56 %). They confirm a shallow estuarine-type environment. *Loxoconcha* and *Xestoleberis* suggest an abundance of *Zostera*.

The sediment is fine-grained quartzose sand with 8–10 per cent shell debris. Except for *Panopea glycymeris* few of the bivalves are articulated. *Panopea* is a deep burrower and would have been protected from disturbance. A dark layer (hydrotroilite) with corroded pollens is situated 0,25 m from the surface of the shell bed. The pollens include many Gramineae, Chenopodiaceae, Cyperaceae, Compositae, (Professor E. M. van Zinderen Bakker, pers. comm.). The Gramineae (grasses) and the Compositae are very varied. Chenopodiaceae is a small plant that thrives in a salt marsh environment in relatively dry climates. Cyperaceae (sedge) indicates the presence of water. These pollens suggest that for a time the site was isolated from open circulation. Hydrotroilite suggests reducing conditions created by restricted circulation.

An excavation to a depth of 10 m just inland of this site shows that the shell bed does not continue landward.

There is evidence in the river bank a few hundred metres west of the homestead of two separate transgressions (sites 13 & 14). The oldest unit consists of a semi-consolidated shelly sand with rounded quartz pebbles, 1 m thick, with a surface 4,5 m a.s.l. The mollusc assemblage which is leached, is characterized by abundance of *Mactra glabrata*. *Solen capensis* occurs articulated. *Loripes liratula* is the only thermophilic mollusc. This bed grades upwards through silty loam to a dune sand. The shelly deposit is most likely a continuation of the 6 m transgression complex.

A shell bed dominated by 'fresh' *Dosinia lupinus* is banked against this older unit up to 3,2 m a.s.l., but extending below river level. At river level there is an extensive oyster reef 50 m in length consisting of *Ostrea algoensis*. Nearer the homestead gypsum deposits indicate former saline conditions with little dilution by fresh water. The younger shell bed reflects a sea level in the vicinity of 3,5 m a.s.l.

Other fossiliferous deposits are exposed on the south bank of the Berg River at Bloemendal (site 11) at 3–4 m a.s.l. and near the bridge at Velddrif. The Bloemendal assemblage, which contains the thermophilic species *Loripes* *liratula* and *Leporimetis hanleyi*, is suggestive of a shallow, sheltered environment (Tankard 1975, table 1). The bridge assemblage is a mixture of sand-dwelling and rock-dwelling forms: *Patella* sp., *Choromytilus meridionalis*, *Dosinia lupinus*, and *Venerupis senegalensis*. Well-rounded cobbles are suggestive of a surf beach.

Withdrawal of the 6,25 m sea left the barrier-beach and bar complex at Velddrif emerged, while a lagoon developed in the area between the bars. Aerial photography (Fig. 15) shows that this area is an old lagoon floor with micro-relief of shallow channels and sand-bars. Several pits into these fine-grained lagoonal sediments enabled the collecting of mollusc fossils (site 8). All the forms were small. '*Rissoa*' constitutes about 90 per cent of the assemblage. The assemblage is typical of a shallow, sheltered environment. *Nassarius*

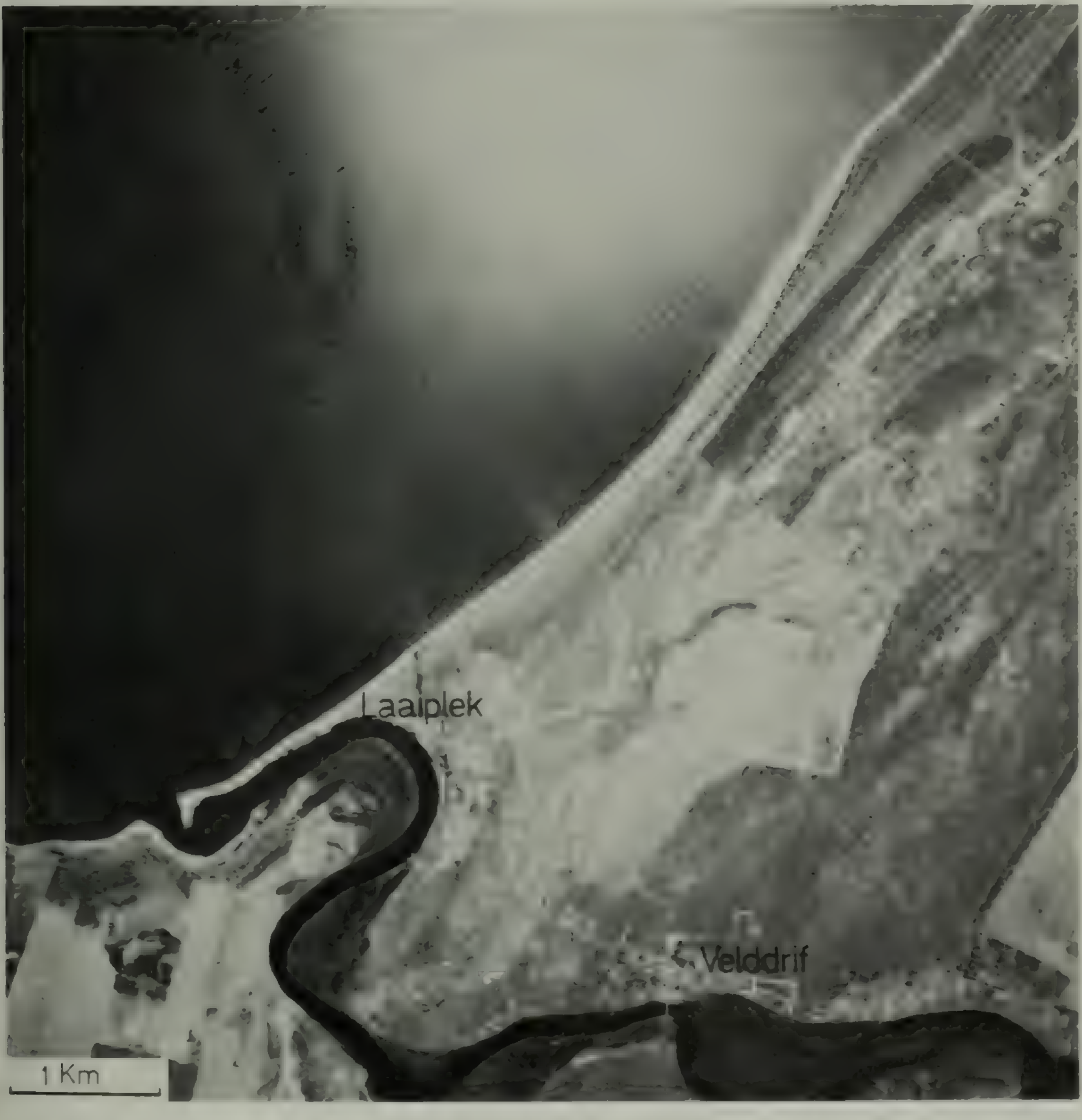

Fig. 15. Aerial photograph showing relict Late Pleistocene lagoon floor between emerged bars at Velddrif. (Aerial photograph reproduced under Government Printer's Copyright Authority 4603 of 2-11-1971.)

kraussianus is abundant in weed-beds at low tide on muddy sands (Day 1969). Other fossils include crab (Brachyura) chelae, echinoid spines, bryozoan remains, sponge spicules, ostracodes, and foraminifers.

The ratio of foraminifers to ostracodes is 34 to 1, indicating free access to the sea. The foraminifer assemblage (Fig. 8, Table 2) is dominated by *Elphidium* sp. (50 %) and *Rotalia beccarii* (46 %). Snider & Curran (1974) have found large numbers of *Rotalia beccarii* and *Elphidium* spp. to characterize the lagoonal environment. The large numbers of tests per unit volume of sediment indicate slow sedimentation rates. Carter (1951) has found that sorting governs the size of the specimens, so that the size of the foraminifer tests would be similar to the sediment grain size. According to Krasheninnikov (1960 quoted in Loeblich & Tappan 1964) large numbers of *Elphidium* indicate mobile water. The tests of the Velddrif (site 8) specimens show no wear or evidence of transportation.

In comparison with other west coast sites the tests of *Rotalia* and *Elphidium* are small, and are present in large numbers. Phleger (1960) has found that under optimum conditions, and in large living populations, small size may be taken to indicate unusually favourable conditions and rapid reproduction.

Cytheromorpha sp. constitutes 49 per cent of the ostracodes, *Loxoconcha peterseni* 21 per cent, and *Perissocytheridea estuaria* 6 per cent. But 8 per cent of the assemblage comprises freshwater forms: *Eucypris* sp. (1 %), and *Paracypretta ampullacea* (7 %), suggesting periodic influxes of fresh water. *Cytheromorpha* can tolerate brackish water. *Loxoconcha* and *Xestoleberis* prefer saline water (Benson 1961) and suggest the presence of marine grasses.

These fossiliferous deposits between the bars are at 1,5 m a.s.l. and must relate to a transgression to about 2 m a.s.l.

Saldanha Bay

Saldanha Bay, the only major inlet on this coast today, has a deep entrance (42 m) which shoals to 2 m at the mouth of Langebaan Lagoon. The bay probably originated by differential erosion of the different granite types and Malmesbury shale. (Drilling operations show the presence of extensive Malmesbury shale north and north-east of the shoreline.) There is no evidence of faulting or of an old river valley.

On the landward side of the Hoedjiespunt peninsula a low plain below 10 m connects Noordbaai with Smitswinkelbaai. Fossiliferous deposits show that this area was probably flooded by the last interglacial sea. The surface of the shelly sands is only 1 m a.s.l. (site 18). The dominant molluscs are *Oxystele variegata* (15,7 %), *Clionella sinuata* (19,0 %), and *Tellimya trigona* (26,1 %). The assemblage is composed of rock-dwelling and sand-dwelling forms, and indicates a shallow environment.

Limestones form a low cliff along the Blouwaterbaai shore (Fig. 16). The oldest unit is an indurated aeolianite which is capped with calcrete. At 2,8 m a.s.l. the calcrete is overlain by 0,6 m of shelly marine limestone which contains angular cobbles of Malmesbury hornfels. The molluscs from this marine

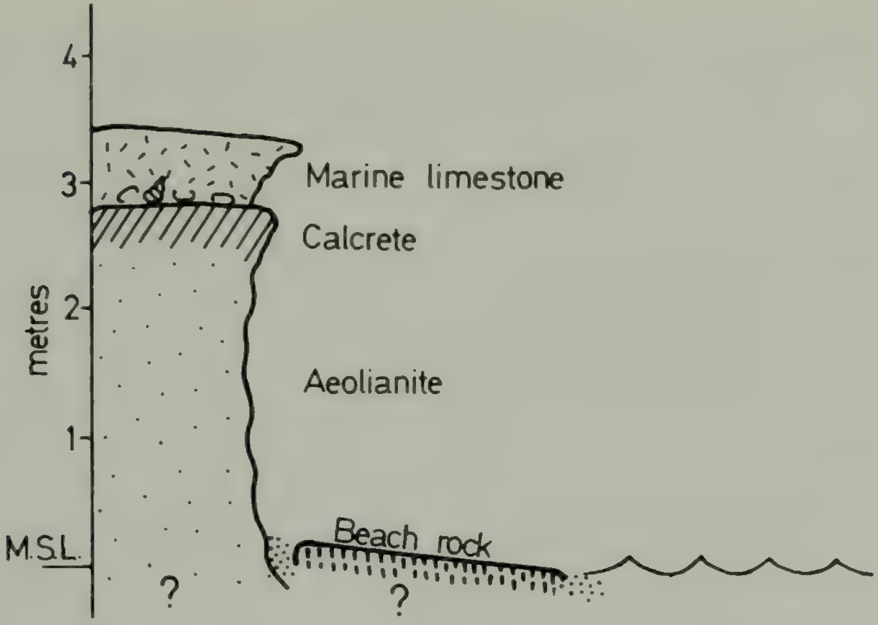

Fig. 16. Typical section through Blouwaterbaai limestones.

unit include rock-dwelling forms such as *Patella* spp., *Burnupena papyracea*, etc., and sand-dwelling forms such as *Turritella capensis*, *Bullia digitalis*, etc. They suggest an intertidal deposit. The youngest unit is a thin pavement of beachrock in the present intertidal zone, and reaches nearly to the foot of the cliff. Beachrock is formed in the intertidal zone.

Langebaan Lagoon

Extensive shell beds along the southern and western shores of the lagoon show that the lagoon is a feature which existed at least by the Late Pleistocene. The lagoon is a north-westerly trending body 15 km long and a maximum of 4 km wide whose present channels are maintained by strong currents generated by the summer south-easterly winds. Where the eastern shore is controlled by granite topography the last interglacial and present shorelines probably coincide. But extensive shell beds on the southern shore on the farms Geelbek, Abrahamskraal, and Skrywershoek, demonstrate a more southerly extension in the Eem.

The lagoon is separated from the Atlantic Ocean by a long ridge that connects Ysterfontein with the South Head granites. One can only surmise that it developed as a prograding spit and tombolo or a barrier-beach complex. Whatever its origin, it was reinforced by dune sand accumulation. The present lagoon is the result of Flandrian flooding of a pre-existing dune landscape.

The Geelbek deposits are a lagoon floor shelly limestone accumulation reaching an elevation of 2 m a.s.l., and overlain by calcrete. The coquina includes quartz porphyry cobbles. Many of the bivalves are still articulated. The mollusc assemblage is indicative of a shallow, sandy substrate, and contains several thermophilic molluscs (Tankard 1975, table 1), for example *Loripes liratula*, *Tellina madagascariensis*, and *Venerupis dura*.

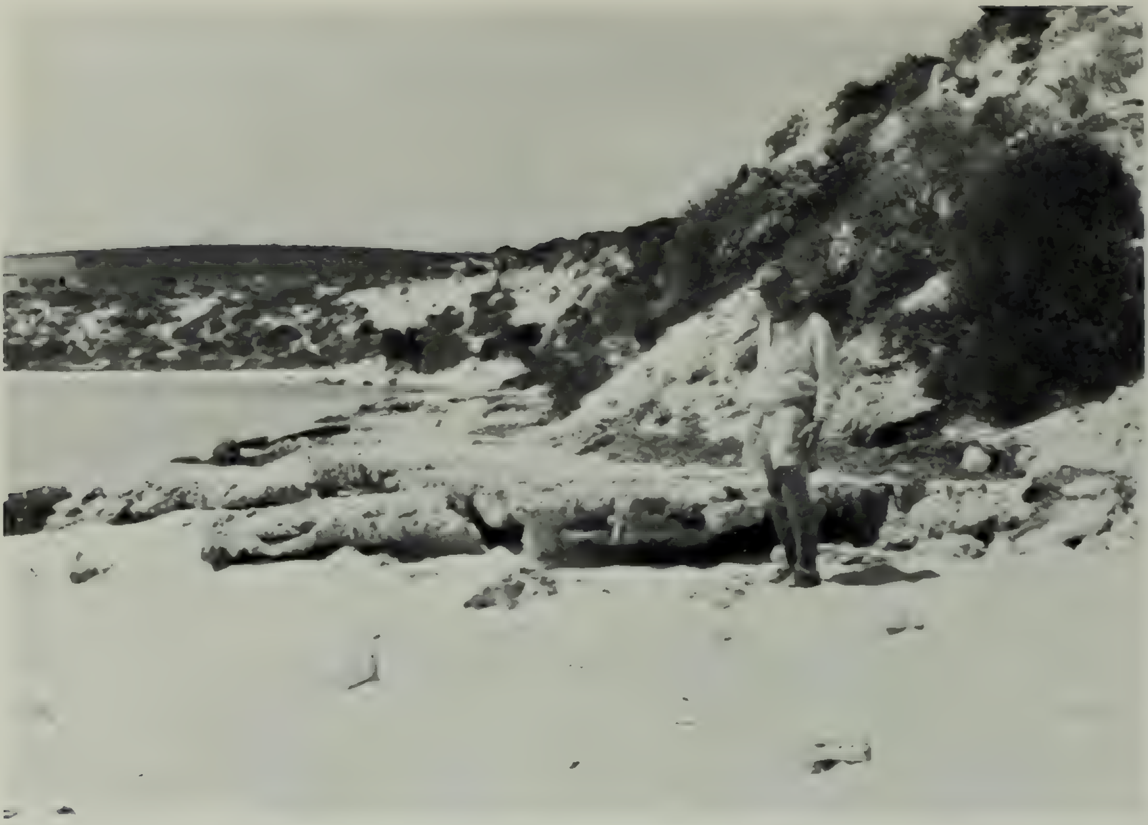

Fig. 17. Planation platform on marine limestone, Churchhaven.

At Churchhaven a shelly limestone has been locally planed at 1,2 m a.s.l. (Fig. 17). Thin-section examination shows the limestone to consist of 90 per cent quartz and 10 per cent detrital shell with drusy calcite cement. All the detritus is fine-grained and well rounded, and both quartz and shell are extensively corroded. Most of the shell grains are molluscan, with only occasional echinoid spines and foraminifer tests. Figure 18, which shows the growth of calcite scalenohedra on the inside of an ostracode carapace (*Urocythereis* sp.), demonstrates the extensiveness of diagenesis in these deposits.

A layer of mollusc shells contains many articulated shells and unbroken valves. They are predominantly shallow water, sand-dwelling forms. *Aurila dayii* and *Aglaiella railbridgensis* are common ostracodes (Fig. 8, Table 2). Ichnofossils include crab-burrows (Fig. 19), and some 2–3 cm diameter vertical burrows, probably *Ophiomorpha* which is attributed to the marine decapod *Callianassa*.

According to Mr B. W. Flemming of the University of Cape Town (pers. comm.) the erosional platform at Churchhaven is part of an extensive platform which he has traced for 100 m off Kraalbaai. At Kraalbaai there is a contact with the marine limestone and overlying aeolianite at 2,5 m a.s.l. (Fig. 20) with bivalve remains at the contact. *Ophiomorpha* are common in the marine limestones at this site. A very interesting trace-fossil that indicates that the top of the marine limestone at Kraalbaai is partly non-erosional is the series of

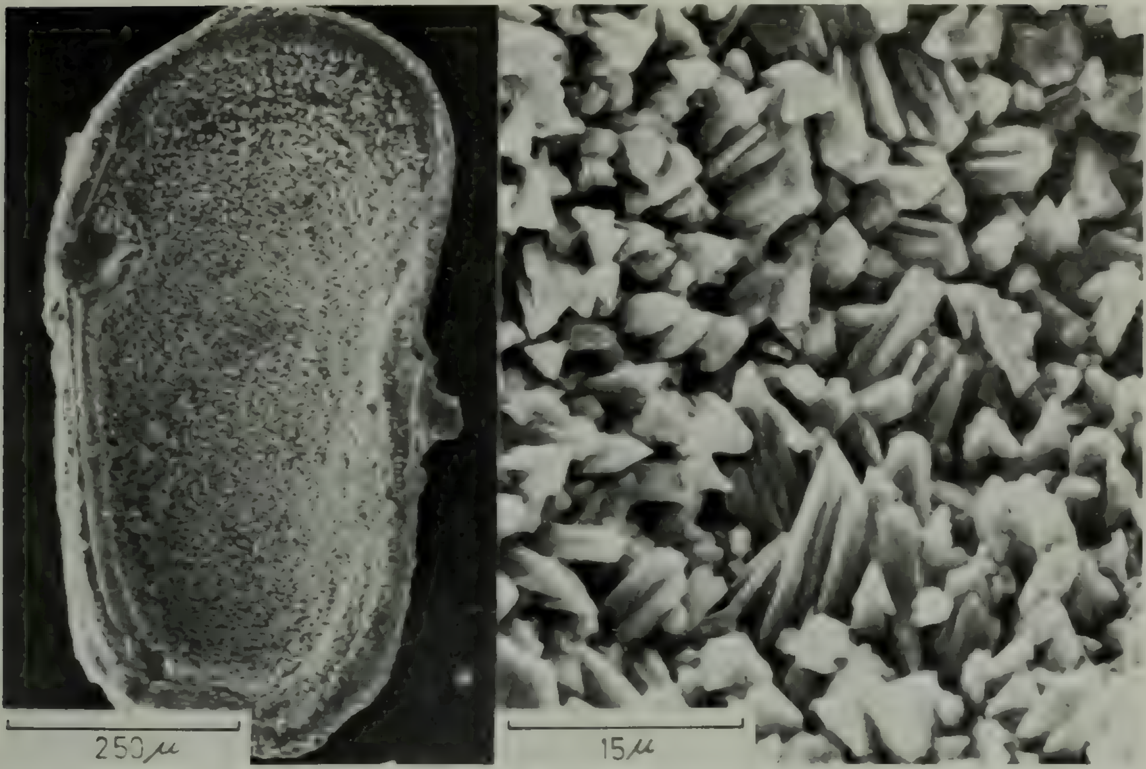

Fig. 18. Calcite scalenohedra on inner surface of ostracode carapace demonstrates extensive diagenesis at Churchhaven.

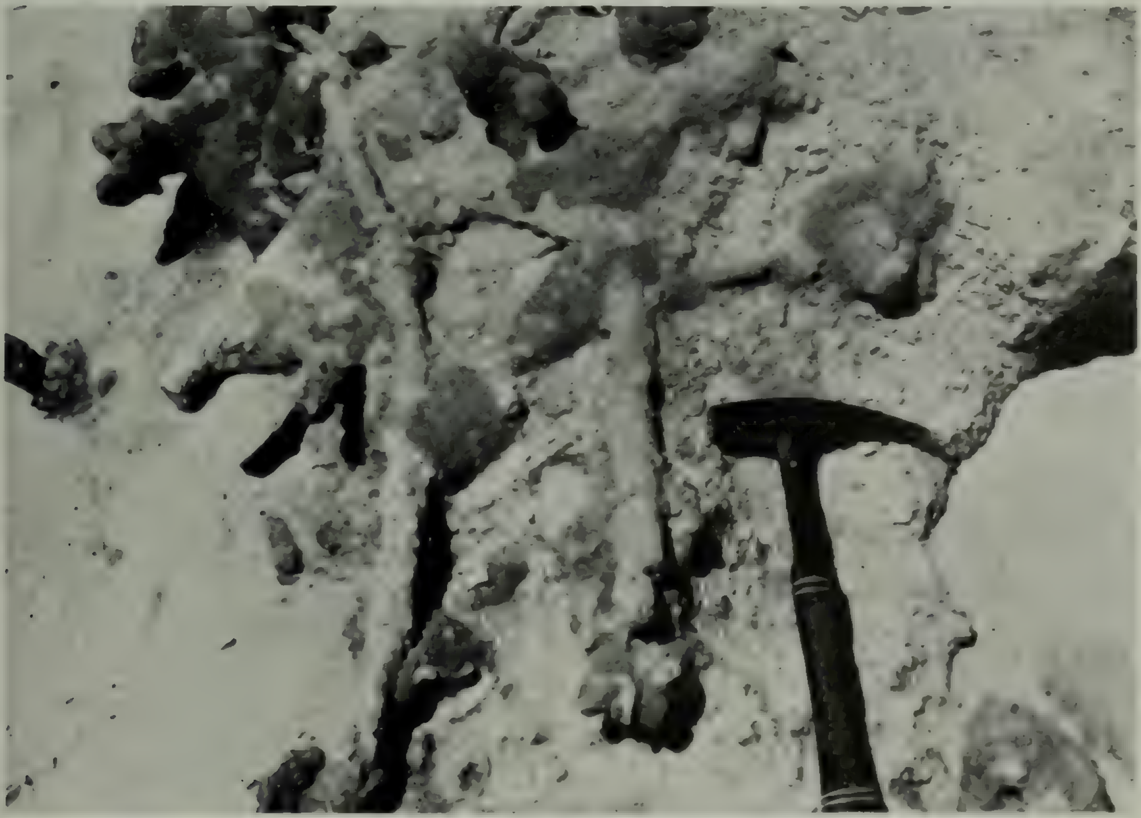

Fig. 19. Crab-burrows associated with marine limestone at Churchhaven.

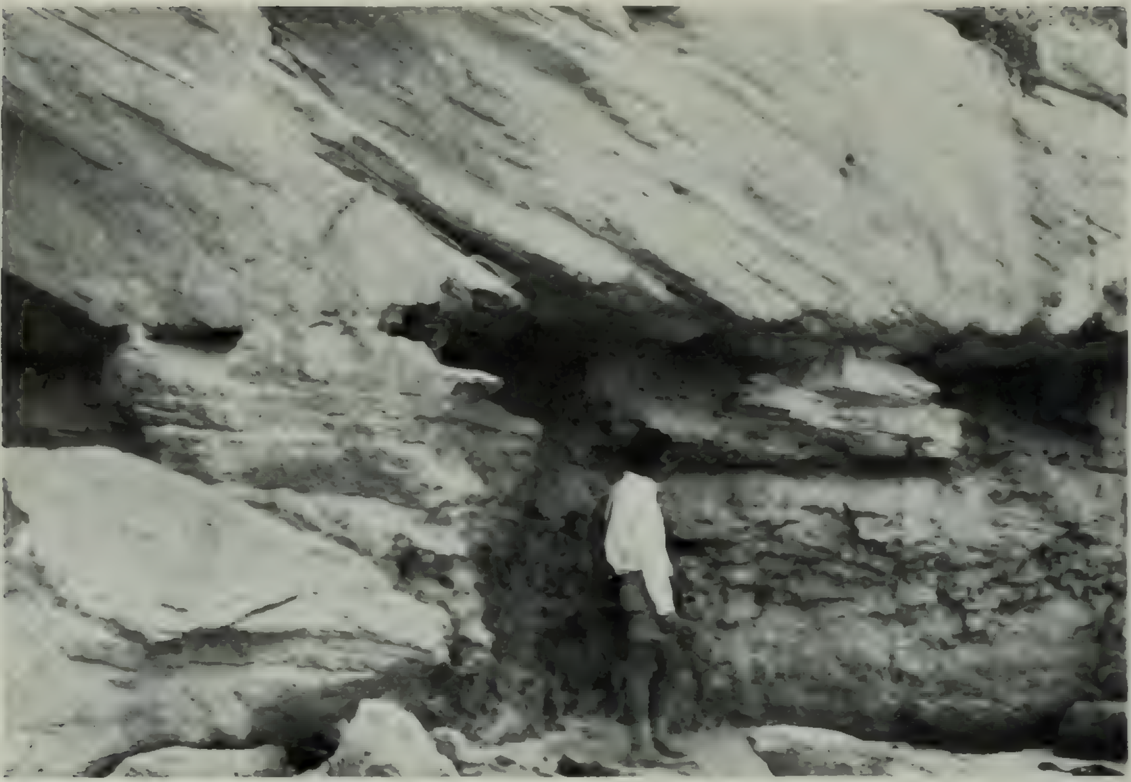

Fig. 20. Contact of marine limestone and aeolianite at Kraalbaai. Note typical beach low-angle cross-stratification below the contact.

footprints of a terrestrial mammal, probably the strandwolf *Hyaena brunnea* (Fig. 21). The preservation of these footprints, the depth of the print, and the detail of the print suggest a wet surface. Ridges of sand on one side of each foot-print demonstrate that the animal was walking on a slope. Together with ripple-marks on the same plane this suggests a wet beach.

That the platform was eroded by another transgression is shown by the sedimentary succession at Churchhaven (Fig. 22). The lower marine limestone platform is overlain by dune sands in which at about 4 m a.s.l. there is an outwash deposit. The outwash consists of cobbles derived from the lower limestone along with mollusc shells. Excavation showed that the platform extends beneath the outwash. The outwash deposit is composed of 90 per cent cobbles and 10 per cent shells (Parker 1968). The shells are mainly disarticulated.

Parker (1968) recognized two distinct units at Churchhaven which he separated accordingly to lithology and the mollusc fossils. He recognized that the lower unit was not a shoreline feature, but a lagoon floor deposit. He believed the outwash deposit to be a 4,3 m shoreline. Davies (1973), on the other hand, recognized only one bed into which a 1,5 m transgression incised.

The outwash deposit occurs at varying altitudes in this region, that at 4 m a.s.l. being the highest exposure. Pie diagrams comparing the mollusc and ostracode assemblages from the two horizons (Figs. 8, 22) confirm Parker's interpretation. But the field evidence shows that the shelly conglomerate is not an *in situ* marine unit, but rather a colluvial deposit that has gravitated

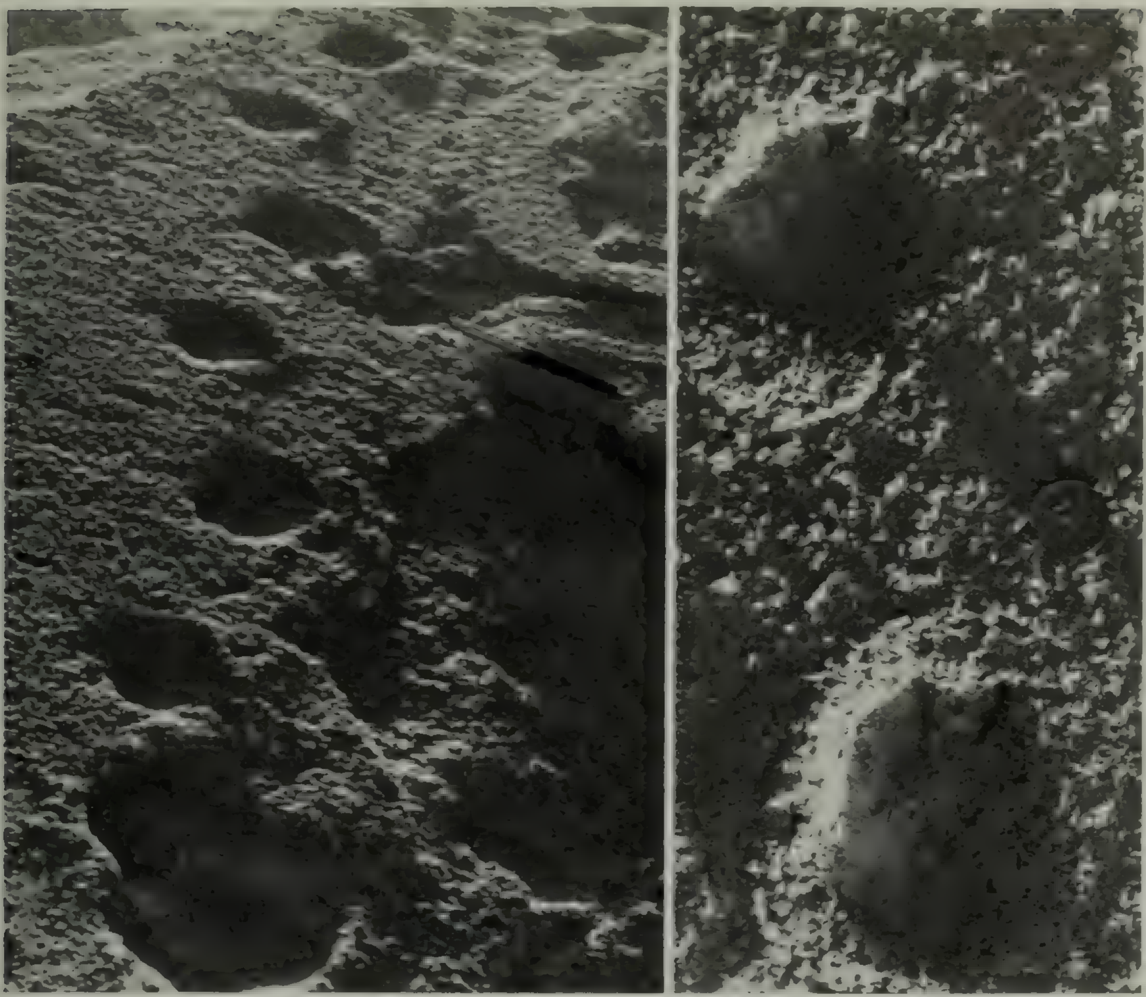

Fig. 21. Mammalian footprints at top of marine limestone Kraalbaai, and detail. Note claw marks in photograph on right.

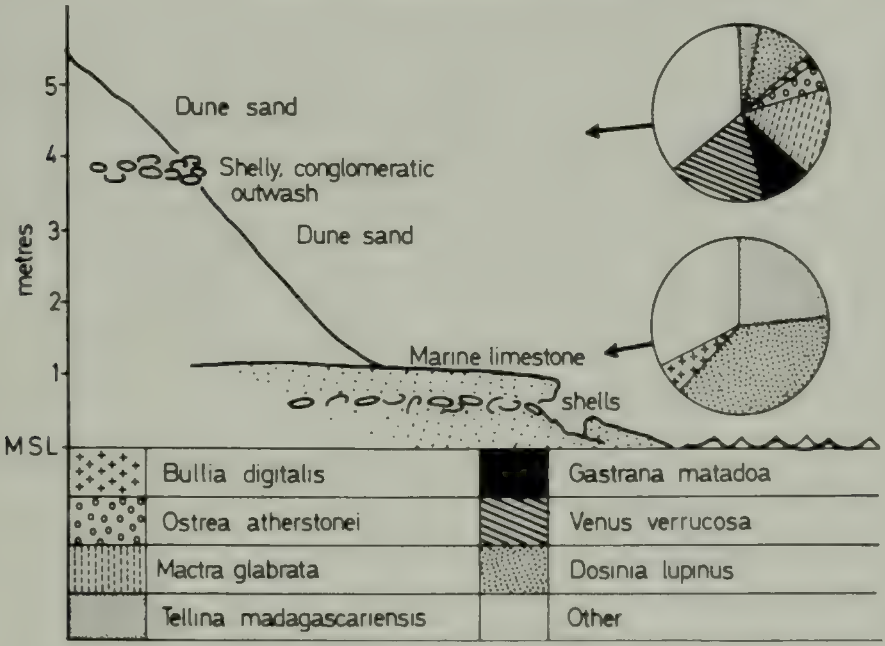

Fig. 22. Sedimentary succession at Churchhaven.

TABLE 3

Radiocarbon Determinations on Samples from the Area between False Bay and the Berg River.

Sample No.	*Locality*	*Altitude* (m)	*Material dated*	*Date* (B.P.)
Pta–094	Kreeftebaai	3–5	shell	40 200 ± 130
–095	Luisterhoek	3–5	shell	48 200 + 2 600 – 2 200
–096	Churchhaven	1,5	shell	48 500 + 3 600 – 2 900
–097	Elandspunt	6,5	shell	41 100 ± 1 200
–098	Elandspunt	6,5	shell	> 49 500
–461	Jutten Point	6–7	shell	2 070 ± 50
–794	Kruispad	5,1	shell	43 700 + 4 300 – 2 700
–796	Kruispad	5,1	shell	39 000 ± 1 860
GrN–5803	Melkbos	4	shell	43 200 + 2 000 – 1 500
–5878	Langebaan Lagoon	–1(?)	shell	6 410 ± 45
I–8372	Milnerton	1,5	shell	33 750 ± 1 780
–	Muizenberg	Inter-tidal	beachrock	25 860 + 1 040 – 1 190
–	Muizenberg	Inter-tidal	beachrock	25 430 + 1 050 1210

(References: Parker 1968; Vogel 1970; Vogel & Marais 1971; Davies 1973; Pta–794 and Pta–796, Dr Vogel pers. comm. 30.1.73; I–8372, Dr B. Kensley pers. comm.; Muizenberg beachrock, Siesser 1974).

down a dune surface. It must therefore reflect a shoreline higher than 4 m a.s.l. Although the higher beach material (outwash) may well contain fossils derived from the lower limestone unit, its mollusc assemblage does appear to be distinct. Furthermore, the shells are fresher.

The conglomeratic colluvium at Churchhaven implies a more vigorous abrasion than occurs along the shores of the present lagoon. Two explanations can be suggested. The first assumes that the peninsula separating the lagoon from the ocean owes its present extent to dune accumulation during the last glacial lowering of sea level. (Evidence will be cited shortly to substantiate this claim.) The width of the tombolo or barrier-beach would have been considerably less than at present. The ratio between the present lagoon width to barrier width is 2:1, whereas the world average is 6:1 (Tanner 1960). A sudden rise of sea level, as suggested at Churchhaven, could have partially breached the barrier, or pushed it back, and reworked the lower limestone. The mollusc and ostracode fauna in the colluvium demonstrates that sheltered lagoonal conditions did exist at some stage during this sea level rise.

An alternative explanation could be that the breach of the barrier took place further north where Kraalbaai is connected with the ocean by a low area. But it is doubtful that this would have created the vigorous abrasion at Churchhaven. Besides, this gap may be the last remaining evidence of more extensive breaching or flooding of the original barrier.

For several years oyster deposits (*Ostrea atherstonei*) have been commercially dredged from the floor of the lagoon where there are reputed to be reserves of 3 million metric tons. East of Kraalbaai they form a layer 1–3 m thick 5,5 m beneath the lagoon surface. Oysters generally settle on a hard substrate and it is possible that initial colonization took place on the limestone platform. *Ostrea atherstonei* valves are common in the Geelbek and Skrywershoek deposits as well as among the colluvium at Churchhaven, but rare in the older limestone. The lagoon floor oyster deposits would most likely correlate with these last interglacial deposits which in turn are correlated with a climatic peak at that time (Tankard 1975).

Age of the Deposits

Assessing the age of these deposits depends upon the assumption that they are primarily of glacio-eustatic origin, and that they can be regionally correlated. Despite the evidence for substantial down-warping in the Pleistocene, there is good reason to believe that tectonism has been minimal in the last 100 ka or so, and that shorelines below + 7 m can be correlated.

Table 3 summarizes the available ^{14}C dates pertaining to former sea levels between present sea level and + 7 m between Muizenberg (False Bay) and the Berg River. All the dates except Pta—461 and GrN—5878 are greater than 20 ka.

Mörner (1971) discusses some of the difficulties of dating shell material older than 15 ka. Miniscule contamination of shells older than 20 ka will give completely spurious dates (Fairbridge 1971). Glacio-climatic evidence shows that any interstadial glacio-eustatic sea levels close to present sea level or higher are unlikely (Fairbridge 1971; Mörner 1971; Thom 1973). All of the dates shown in Table 3 greater than 20 ka would be pre-last glacial.

Only two dates (Pta—461 and GrN—5878) are comparatively young. The date of 2070 B.P. (Pta—461) was derived from *Patella argenvillei* which appears to have been surface collected from a heavily vegetated rampart at 6–7 m a.s.l. (Davies 1973). Even if reliable this date would hardly date the rampart; Davies mentions the 'high throw' of waves along this coast in connection with the ramparts. The other date (6410 B.P.) was derived from an *Ostrea atherstonei* valve dredged from the southern end of Langebaan Lagoon. This date would appear to be too young because sea level would only have recovered by 5,5 ka (Godwin *et al.* 1958). Furthermore, 3 million metric tons of shells implies a lengthy period of accumulation and optimum conditions for reproduction which would be better satisfied in the last interglacial. Flandrian transgression sediments and their mollusc fossils at an equivalent depth below present sea level show that water temperatures in Saldanha Bay in the mid-Holocene were no warmer than at present. The Bomgat bed is probably a Holocene feature (date 3,5 ka, Mr B. Flemming, pers. comm. January 1976).

Available ^{14}C measurements indicate that the marine deposits are mostly older than the range of this technique, and suggest a pre-Weichselian age. The mollusc fauna indicates an Eem age. Composition of the fauna compared with older Pleistocene faunas suggests a comparatively young age. Abundance of thermophilic forms correlates best with the warm isotopic substage 5e peak of deep-sea cores (Shackleton 1969) which occurred at 100–120 ka. Chappell (1974*a*) points out that the widely recognized shoreline between 2 and 7 m a.s.l. in areas remote from plate boundaries, and dated as 120–130 ka, is becoming widely used as a Late Pleistocene sea level datum.

The higher shorelines up to 6,25 m a.s.l. would thus date to about 120 ka, although the lower shorelines nearer present sea level may be younger. In Die Kelders cave on the south coast wave generated boulders are preserved up to 2 m a.s.l. in an erosional strike-passage in steeply dipping Table Mountain sandstone. Occupation of the cave by Middle Stone Age people followed soon after withdrawal of the sea and serves to date the boulder bed as pre-Weichselian, but not much older. Since the boulder bed would have arisen from wave surges through the passage it probably reflects a sea level close to the present and would correlate with the intertidal beachrock at Muizenberg described by Siesser (1974). An immediately pre-Weichselian age, about 80 ka, is suggested for these lower units.

RECENT

Figure 23 summarizes the stratigraphy revealed in an excavation 100 m from the Saldanha Bay shoreline at 18°E. Cross-bedded units of medium and fine-grained sands with articulated *Perna perna*, and suggestive of shoreface sedimentation, form the lowest bed from −4 m to −3,4 m. This passes upwards into horizontally laminated fine sand and coarse sand with *Perna perna*, a typical fining-upward beach sequence. There is a gradual coarsening of the sediment to −1,4 m suggestive of a temporary regression. Shells are more fragmented, and the bivalves disarticulated. The assemblage is an intertidal sand-dwelling one. A period of pedogenesis resulted in calcrete formation. The calcrete is again overlain by a fining-upward shelly sand due to a final transgression.

The molluscs include: *Turritella capensis*, *Burnupena papyracea*, *Bullia digitalis*, *B. laevissima*, *Clionella sinuata*, *Petricola bicolor*, *Perna perna*, *Scissodesma spengleri*, *Lutraria lutraria*, *Donax serra*, and *Venerupis senegalensis*.

Drilling operations on the coastal flats adjacent to Saldanha Bay have shown the widespread occurrence of shelly sands and shelly limestones, with intercalated calcrete horizons, below sea level datum. Furthermore, several boreholes into the bay floor north of Hoedjiespunt penetrated a peat at −22 m which was preserved beneath calcrete (Mr A. De La Cruz, pers. comm.).

FLUVIAL SEDIMENTS

At several localities from Cape Town to Verlorevlei there is evidence of considerable fluvial activity in the past. These sediments are presumably of

Pleistocene age, although extensive deltaic sediments on the continental shelf between Dassen and Robben Islands have been assigned to the Lower Tertiary (Dingle 1971*b*).

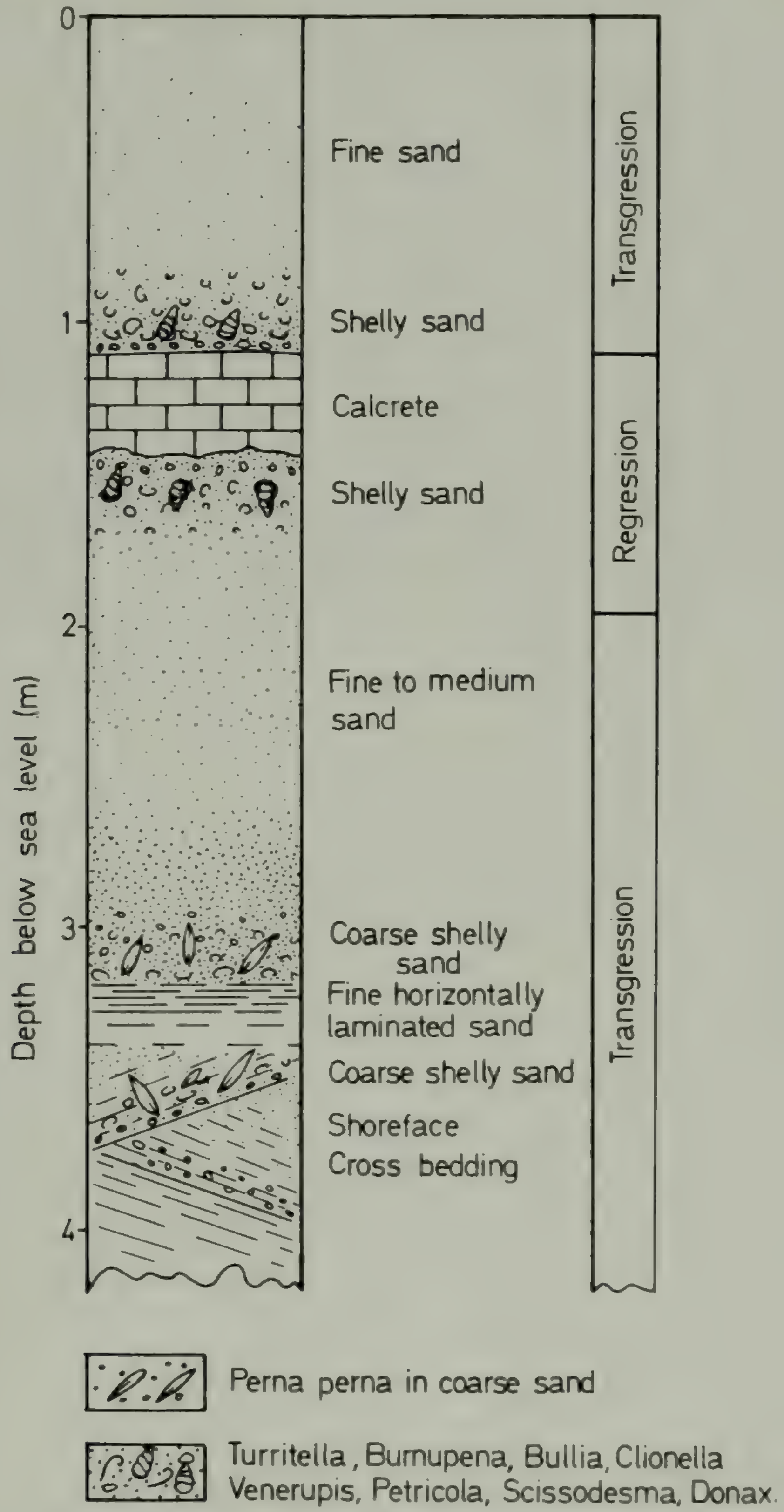
0
1
2
3
4
Depth below sea level (m)
Fine sand
Shelly sand
Calcrete
Shelly sand
Fine to medium sand
Coarse shelly sand
Fine horizontally laminated sand
Coarse shelly sand
Shoreface
Cross bedding
Transgression
Regression
Transgression
Perna perna in coarse sand
Turritella, Burnupena, Bullia, Clionella
Venerupis, Petricola, Scissodesma, Donax.

Fig. 23. Flandrian sedimentary succession at Saldanha.

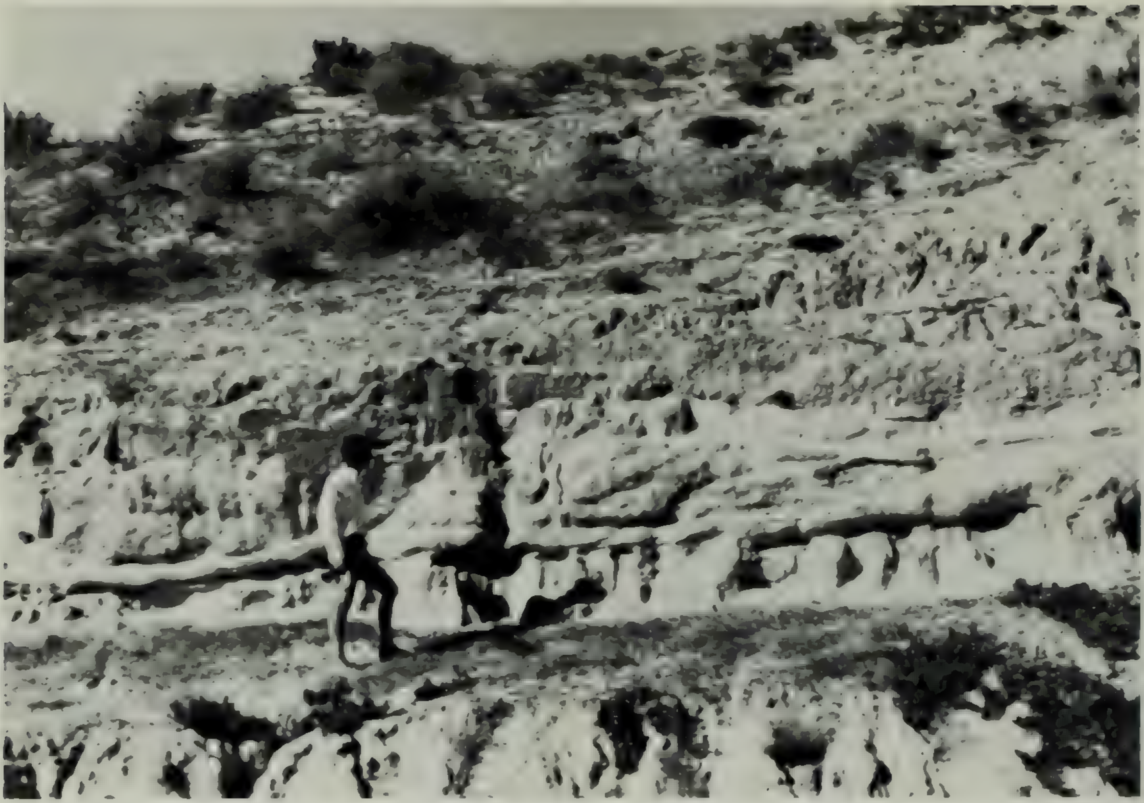

Fig. 24. Relict fluvial sediments at head of Verlorevlei.

The planed surface of the Malmesbury Group at 30 m a.s.l. east of the Sout River is an old river terrace and is mantled with angular gravel (the farms Maatjesfontein and Hamburg in the Hopefield area).

Tankard (1974) has discussed in detail fluvial sediments at Langebaanweg, the Baard's Quarry deposits. The deposits of the northward draining channels were mineralized by phosphate derived from the Varswater Formation. The mammal fossils suggest an Early Pleistocene age.

At Ysterplaat (Cape Town) an exposure of cross-bedded, rounded, quartz gravel is suggestive of a point-bar deposit, while opposing dips laterally separated through the section suggest a meandering stream. Another exposure through relict fluvial sediments occurs at Redelinghuis (Fig. 24) at the eastern extremity of Verlorevlei (26 km from the mouth). Here at least 18 m of river sediment occupy an old channel with a thalweg less than 6 m (concealed) above vlei level. The sediment is predominantly fine-grained, iron-stained, quartzose sand, with lenticular, gravelly, channel lag deposits which show some imbrication of the pebbles.

Extensive fossiliferous deposits demonstrate that the ancestral Berg River valley cutting was pre-Eem. Consolidated fluvial gravels and bog-iron-ore are exposed in the bank at Swartjiesbaai. Weichselian lowering of sea level to —130 m lowered the controlling base level of the Berg River. Visser & Schoch (1973) mention four boreholes for the Velddrif bridge foundations which intersected at least 4,3 m of conglomerate beneath a 5 m cover of shelly sands which probably originated during the Flandrian rise of sea level.

AEOLIANITES

The coastal plain is covered with a veneer of dune sands and aeolianites. Du Toit (1917) referred to the aeolianites as *Dorcasia* limestone, while Visser & Schoch prefer the name Langebaan limestone since the common fossil land-snail is *Trigonephrus globulus* and not *Dorcasia*. These authors present a lengthy discussion of the aeolianites.

Several exposures suggest that the aeolianite may range in age back to the Neogene. In a quarry 4 km north of Saldanha high-angle cross-bedded aeolianite overlies marine Bredasdorp Formation rock of probable Miocene age. Behind the President Jetty on Saldanha Bay a well-lithified, fine-grained aeolianite underlies younger aeolianites.

Most of the aeolianites appear to be much younger, and probably accumulated during the last glacial lowering of sea level when vast tracts of unvegetated sand lay exposed on the emerging sea floor. Several occurrences of interbedded outwash suggest that the climate was not necessarily arid. Cross-bedding azimuths at Kraalbaai (mean 360°) show that a southerly wind was prevalent. Rogers & Du Toit (1909) describe a well at Paternoster which penetrated sandy limestone containing land-snail shells and tortoise bones to 21 m below sea level. Tankard & Schweitzer (1974) have described the former seaward extension of dunes in the Die Kelders area, and also mention *in situ* Middle Stone Age artefacts in the outwash deposits which shows that there the aeolianites must be Weichselian or younger. Furthermore, limestone blocks in the cave show that lithification of the aeolianites occurred prior to about 6 000 B.P. Similar inter-bedded outwash deposits containing Middle Stone Age artefacts occur as far north as Saldanha. A single ^{14}C assay on ostrich eggshell from a midden in the limestones behind the Sea Harvest factory gave an age greater than 40 000 years (UW 282).

An interesting feature of the coastal limestones are the solution-pipe cavities which have formed by karst weathering. At Churchhaven and Velddrif they penetrate the last interglacial marine limestones and shell beds. The pipes are 0,3–0,8 m in diameter and vertical. At Churchhaven they are marked by a 3 cm thick lithified crust. All the pipes are filled with non-calcareous terrestrial *terra rosa* type sediment. Blackburn *et al.* (1965) described an identical situation from Australia and suggest that they arose from solutional weathering and the filling of the voids with sediment by simple gravitation. The *terra rosa* sediment together with the karst weathering and colluvial deposits suggest a wetter climate in the south-western Cape in the last glacial.

Extensive Late Stone Age shell middens overlie the Langebaan limestone on the North and South Heads. On the South Head the midden is in part calcretized.

PROPOSED NEW LITHOSTRATIGRAPHIC NAMES

The Bredasdorp Formation comprises a variety of limestone types of marine and aeolian origin. It includes marine limestone with conglomerate and coquina horizons, and beds consisting mainly of whole shells. The major part of the formation consists of dune sand and 'shell grit and locally grades into pure shell-beds; it has been calcified into rocks varying from crumbly calcareous sandstone to hard, crystalline limestone. . . . Solution channels are often encountered in the limestone' (Spies *et al.* 1963). Lithologically this description describes the marine and aeolian limestones and shell beds of the Saldanha area. Although locally the limestones may be indistinguishable lithologically, it is usually possible to separate the aeolian and marine components. Two members of the Bredasdorp Formation are here defined:

1. Velddrif Member: the type-section is the bar exposure at Velddrif (Figs 12–13). Lithologically it consists of unconsolidated beds of shell and comminuted shell, locally cemented, and with little quartz. But it ranges through limestones with shell layers to coquina, for example at Churchhaven.
2. Langebaan Limestone Member: type-section on Hoedjiespunt behind the Sea Harvest factory where it is over 20 m thick. It consists of fine to medium-grained calcareous sand and limestone with fine shell detritus and complete shells of the land-snail *Trigonephrus globulus.* This land-snail is distinctive enough to feature as a lithological component. The member includes outwash horizons and Middle Stone Age middens.

CONCLUSIONS AND SYNTHESIS

Tilting and warping since the Miocene have displaced marine units from their original elevations, so that the equivalent of the Namaqualand 45–50 m transgression complex (Carrington & Kensley 1969) is situated at only 10 m a.s.l. in the Saldanha area. Sediments equivalent to the Namaqualand 17–21 m transgression complex are possibly submerged in the Saldanha area. But there is good reason to believe that warping has been minimal in the Late Pleistocene.

Evidence for stillstands of the sea in the last interglacial are not always unequivocal. There is no difficulty in recognizing shorelines, but it is frequently difficult to discriminate between major stillstands and lesser features. In summary, data from the south-western Cape identifies three stillstands of the sea in the last interglacial, with the shoreline at 6,3 m a.s.l. being a major feature. These stillstands are at 6,3 m a.s.l. (C I), 2–3,5 m a.s.l. (C II), and sea level (C III).

The platform on the seaward edge of the Vredenburg pluton was carved partly in the Neogene, remodelled in the Early Pleistocene, but owes its present relief to Late Pleistocene abrasion. Relief of the platform is such that it could have been carved by a single stationary sea level. The outer ramparts on the North Head and South Head platforms were formed by a sea level in the region of 6,3 m a.s.l. Shell beds on the platform agree with this interpretation. Similarly shell beds on the Malmesbury platform west of the Berg River mouth are related to a major stillstand at 6,3 m a.s.l., as are the extensive barrier-beach and breaker-bar complex of the St. Helena Bay coastline. That there are few indications of lower last interglacial shorelines along the open coast suggests that this stillstand was a major one.

Shell deposits in the former Verlorevlei and Berg River estuaries have maximum elevations of 5 m a.s.l. Infratidal molluscs still in their living positions suggest a mean sea level at least at 6 m a.s.l. But the fauna in general, which in estuaries would inhabit the mid-tide to low-tide zone (Emery & Stevenson 1957), shows that this sea level could not have been much above 6 m, and thus agrees with the C I transgression.

Evidence for a transgression to 2–3,5 m (C II) consists of a shell bed which is banked against older C I sediments on Kruispad, the lagoon sediments between the emerged bars at Velddrif, Blouwaterbaai sediments, Geelbek tidal flat sediments at 2 m a.s.l., and the Kraalbaai aeolianite-marine limestone contact at 2,5 m a.s.l.

A boulder bed in the Bomgat on the Hoedjiespunt peninsula obviously owes much of its present elevation to waves surging up the passage through the granite in front of the cave. Considering that the elevation of this boulder bed is only 3,5 m a.s.l. it could be attributed to very heavy surf during high tides. The 'fresh' appearance of the shells which still have their colour preserved would suggest a Recent age, and the elevation is certainly not excessive given the physical setting of the cave. Samples were submitted for radiocarbon dating even though groundwater contamination seems likely. A date of 3,5 ka suggests a Holocene rather than a last interglacial origin. This site illustrates some of the difficulties encountered in raised shoreline studies.

At four sites there is evidence for a sea level in the last interglacial coinciding with the present beach (C III). This includes beachrock at Muizenberg (Siesser 1974), Blouwaterbaai, and Jutbaai. Wave-generated boulders beneath Middle Stone Age sediments in Die Kelders cave are attributed to waves surging into the cave from about the present position of sea level.

These results are summarized in a graph of Late Pleistocene eustatic sea level changes (Fig. 25). That portion of the curve from about 47 ka to the present is based on ^{14}C dates of submerged material, and will be fully discussed elsewhere. The last interglacial part of the curve agrees well with the shorelines on Mallorca (Butzer & Cuerda 1962). It is suggested that the C I shoreline correlates with their Tyrrhenian (T) IIa, C II with T IIb, and C III with T III. According to Butzer & Cuerda it is the T II shoreline (5–10 m) which contains thermophilic molluscs, and Tankard (1975) has suggested correlation of the C I thermophilic fauna with that sea level. Broecker *et al.* (1968) have dated three Eem transgressions on Barbados: B III (6 m a.s.l.) at 122 ka, B II at 103 ka, and B I at 82 ka, and Chappell (1974*b*) has dated three sea-level peaks on New Guinea at 120 ka, 100 ka, and 80 ka. Alternatively, the thermophilic

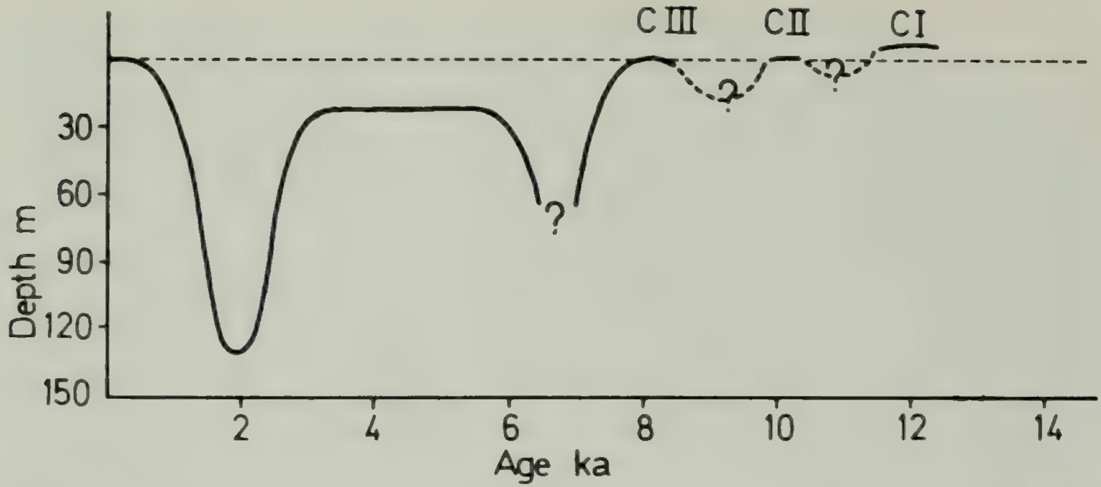

Fig. 25. History of sea level oscillation over last 120 ka shown in graph form. C I = 6,3 m a.s.l.; C II = 2–3,5 m a.s.l.; C III = 0 m a.s.l.

mollusc content of the C I and C II shorelines suggests the distinct possibility that the three last interglacial peaks of the south-western Cape may all correlate with the warm peak at 120 ka, and that the two lower shorelines would then represent only temporary halts in a regression from the 6,3 m level.

It is not known whether the C II and C III shorelines represent temporary stillstands in regression from the major C I stillstand, or whether they are in fact transgressive and separated by regressions.

Withdrawal of the sea with the build-up of high latitude glaciers left vast, unvegetated tracts of sand exposed on the emerging shelves, and these were blown into dune fields by wind systems which may have increased in intensity with the onset of glaciation. But in the south-western Cape they do not signify an arid climate. On the contrary, there is evidence that precipitation was in fact higher than today at times.

There is little evidence to suggest Holocene sea levels much higher than the present.

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6. SYSTEMATIC papers must conform with the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. n., sp. n., comb. n., syn. n., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (*Lembulus*) *bicuspidata* (Gould, 1845)

Figs 14–15A

Nucula (*Leda*) *bicuspidata* Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (figs 8a–b).
Nucula largillierti Philippi, 1861: 87
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

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(continued inside back cover)

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ANCHISAURUS CAPENSIS (BROOM) AND A REVISION OF THE ANCHISAURIDAE (REPTILIA, SAURISCHIA)

by

P. M. GALTON & M. A. CLUVER

Cape Town Kaapstad

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By

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M. A. CLUVER

South African Museum, Cape Town

(With 13 figures and 3 tables)

[*MS accepted 22 October 1975*]

ABSTRACT

A complete description of the skeleton of the type specimen (SAM-990) of the prosauropod dinosaur *Gyposaurus capensis* Broom is given. Comparison with other prosauropods indicates that this dinosaur represents a valid South African species of *Anchisaurus* Marsh, 1885 from the Upper Triassic of North America. It is considered that the infra-order Prosauropoda should be divided into three families, viz. Anchisauridae, Plateosauridae and Melanorosauridae. It is proposed that the family Anchisauridae be restricted to prosauropods with relatively slender feet, and that broad-footed forms previously assigned to the Anchisauridae be transferred to the Plateosauridae. The Family Anchisauridae is therefore considered to include the genera *Anchisaurus*, *Efraasia*, *Thecodontosaurus* and several indeterminate species. The genera *Ammosaurus*, *Aristosaurus*, *Massospondylus* (including *Gryponyx*, *Aetonyx* and *Dromicosaurus*), and *Lufengosaurus* (including *Yunnanosaurus*) are included in the Plateosauridae, while *Arctosaurus* and *Ischisaurus* are referred to the suborder Theropoda. '*Thecodontosaurus*' *gibbidens*, *Spondylosoma absconditum* and *Teleocrater alphos* are placed within the Thecodontia, and *Tanystropheus primus* and *T. latespinatus* in the order Lacertilia. Thus constituted, the family Plateosauridae becomes the dominant and most widespread prosauropod family, while the Anchisauridae, in contrast, is known from a geographically and numerically restricted fossil record.

CONTENTS

PAGE

Introduction 122
Redescription of *Anchisaurus capensis* (Broom) 124
  Vertebral column 124
  Pelvic girdle 126
  Hind limb 129
Slender and broad-footed Prosauropods 131
Systematic discussion 132
  The Family Anchisauridae 132
  Anchisauridae *nomina dubia* 141
  Prosauropod species incorrectly assigned to Anchisauridae . 143
  Prosauropoda *nomina dubia* 150
  Non-prosauropod species incorrectly assigned to Anchisauridae 150
  Notes on the Families Anchisauridae and Plateosauridae . 153
Summary 155
Acknowledgements 155
References 156
Abbreviations 158

Ann. S. Afr. Mus. **69** (6), 1976: 121–159, 13 figs, 3 tables.

INTRODUCTION

Broom (1906) described a specimen (SAM-990) from the Cave Sandstone, Stormberg Series (Upper Triassic) of Ladybrand, Orange Free State, South Africa, and referred it to the prosauropod taxon *Hortalotarsus skirtopodus* Seeley, 1894. The holotype of *Hortalotarsus skirtopodus* was referred to the genus *Thecodontosaurus* Riley & Stutchbury, 1836, by Huene (1906) as *T. skirtopodus* and, because SAM-990 differed in several aspects from *Thecodontosaurus*, Broom (1911) made it the holotype of *Gyposaurus capensis*. Broom (1906) noted several resemblances between SAM-990 and *Anchisaurus* Marsh, 1885, from the Upper Triassic of North America, so he referred *Gyposaurus capensis* (SAM-990) to the Family Anchisauridae Marsh, 1885. Galton (1973, in press) provisionally accepted the validity of *Gyposaurus capensis* but noted that the holotype should be carefully compared with *Anchisaurus polyzelus* (Hitchcock) to determine whether or not these species are generically distinct. A comparison of photographs of SAM-990 with a specimen of *Anchisaurus polyzelus* (YPM 1883) showed that *Gyposaurus* is a junior synonym of *Anchisaurus* and that SAM-990 should be redescribed.

Huene in several papers between 1906 and 1932 made important contributions to an understanding of the Family Anchisauridae (as Thecodontosauridae Lydekker, 1890). Charig *et al.* (1965) considerably enlarged the family by referring to it genera of Triassic theropods (Family Gryponychidae = 'Palaeosauridae') based solely on postcranial material which was indistinguishable from that of prosauropods. The generic list of Romer (1966: 370) includes these changes and the comprehensive list given by Steel (1970) faithfully but rather uncritically records all the genera and species referred to the family.

A taxonomic revision of the Family Anchisauridae is necessary for several reasons:

1. Several of the suggested and generally accepted synonymies are probably incorrect. In assessing these the recognition of slender- and broad-footed types (Galton 1971, 1973, in press) is useful.

2. The skeletal anatomy of prosauropods is remarkably uniform, so taxa should be based on specimens which include either most of the specimen or bones which are diagnostically different from those of other prosauropods. Because of the limited number of skeletal variations it is necessary to diagnose taxa on the basis of a combination of characters which, if each was taken in isolation, would not be diagnostic. Unfortunately several of the taxa listed by Steel (1970) are based on specimens which are generically and specifically indeterminate.

3. The group has been over-classified and insufficient account has been taken of the range of individual variation possible within a dinosaurian species; this can be quite extensive, as shown by the prosauropod *Lufengosaurus huenei* Young (see Rozhdestvensky 1966) and the ornithopod *Hypsilophodon foxii* Huxley (see Galton 1974).

4. A few of the taxa included within the family are not prosauropods.

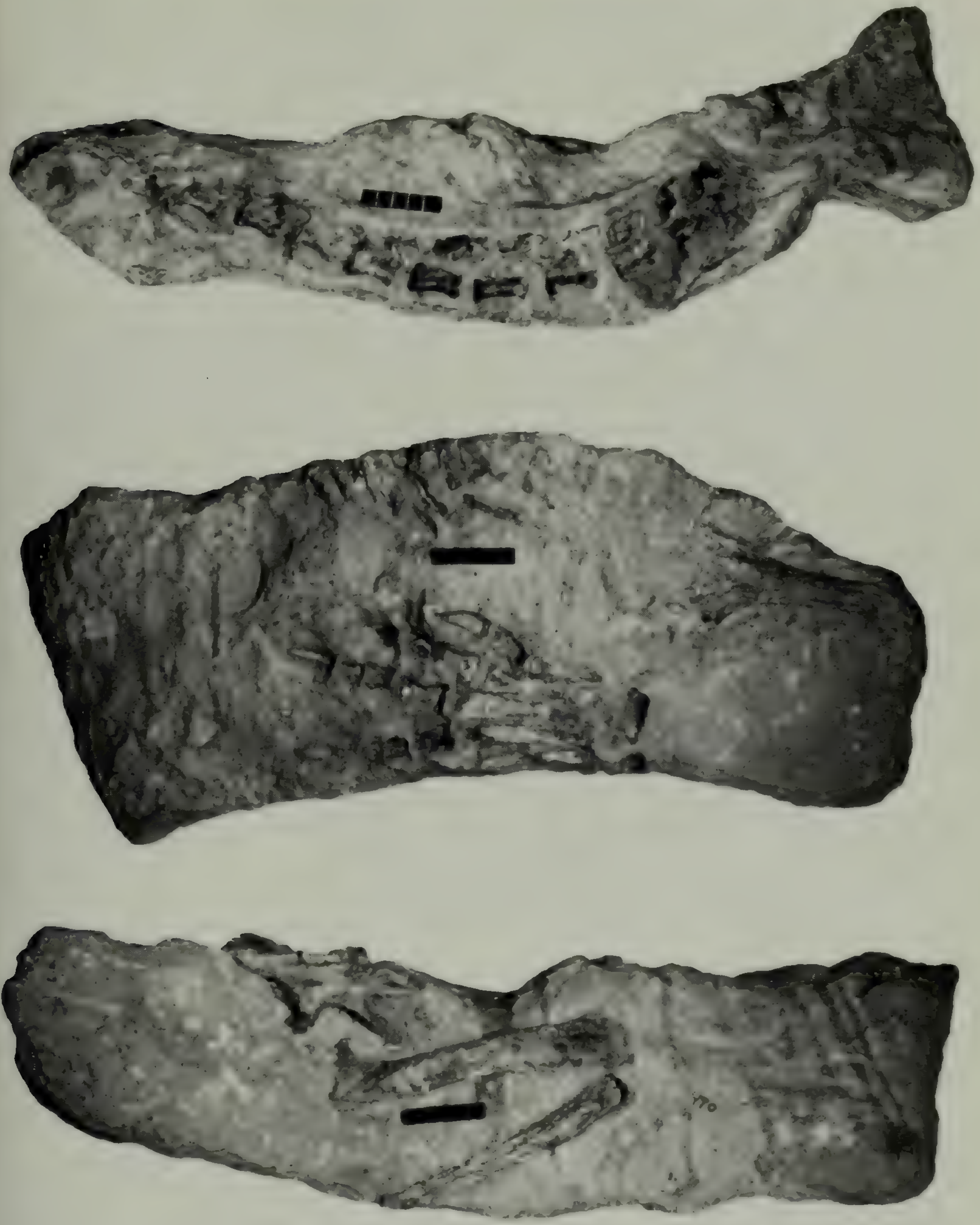


Fig. 1. *Anchisaurus capensis* (Broom). Type specimen (SAM-990) showing vertebral column (top), pubis, ischia and pes (middle) and ilium, femur and fibula (bottom).

Summaries of certain aspects of the revision of the family Anchisauridae have been published earlier (Galton 1971, 1973, in press). The first author (P. M. G.) is responsible for all sections except the description and illustration of SAM-990, which is the work of the second author (M. A. C.).

REDESCRIPTION OF *ANCHISAURUS CAPENSIS* (BROOM)

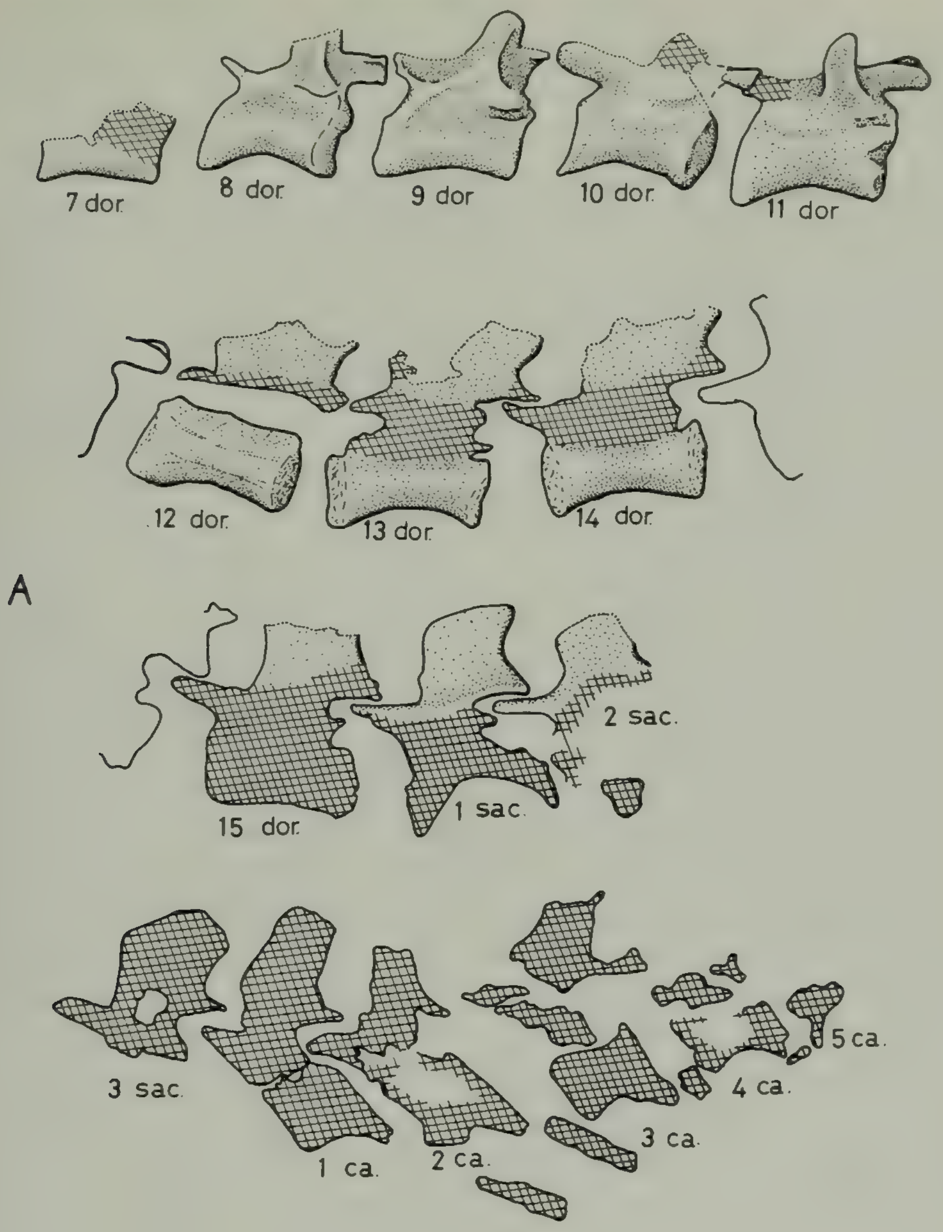
The specimen (SAM-990) is preserved in a soft sandstone matrix (Fig. 1). The bone is generally not well preserved and is inclined to crumble during preparation. Much of the specimen (including most of the vertebral column) is preserved as bone impression, and details of certain of these portions were obtained from silicone rubber positives. Chief portions of the preserved skeleton are 17 vertebrae (including, probably, dorsals, sacrals and caudals), an incomplete left pubis, the right ilium and pubis and both ischia, and the right femur, fibula and pes. Several other fragmentary bones, mostly seen as impressions, are scattered through the block: anteriorly a portion of the right scapula blade can be made out, while impressions of 13 ribs lie ventral to the dorsal vertebrae.

VERTEBRAL COLUMN (Fig. 2)

Altogether 17 vertebrae are preserved, some very incompletely. Eleven of these are in articulation and consist of a number of dorsals and possibly two sacrals. A space separates the last of these from the first of the posterior group, which have been displaced to the right of the anterior series. The space is sufficient to accommodate three vertebrae of the size of those on each side of it, and there is thus the possibility that this gap was originally filled by three sacral vertebrae. However, as will be shown below, it is more likely that a parting of the vertebral column between two sacral vertebrae occurred prior to fossilization of the specimen.

The anterior three vertebrae, imperfectly seen, are not in natural articulation, although still in relatively close association with each other. The centrum of the second vertebra is opisthocoelous and slightly convex anteriorly, while the third centrum is concave anteriorly and posteriorly. The fourth vertebra has a procoelous centrum and is markedly convex posteriorly. This convex rear meets the apparently convex anterior surface of the fifth vertebra's centrum, which also appears to be opisthocoelous. The sixth vertebra is provided with a biconcave centrum, the neural spine is broad in lateral view, and its posterodorsal edge overhangs the postzygapophysis so that a posterior embayment is formed above the postzygapophysis. The seventh vertebra resembles the sixth and the succeeding eighth in the shape of the neural spine, and both the seventh and eighth vertebrae have biconcave centra, similar to that of the sixth vertebra. The eighth vertebra shows the neural spine clearly, and probably represents the condition which existed in the less complete sixth and seventh vertebrae. The spine, posteriorly situated, is antero-posteriorly lengthened and fairly low.

The neural spine of the ninth vertebra is shorter antero-posteriorly. The



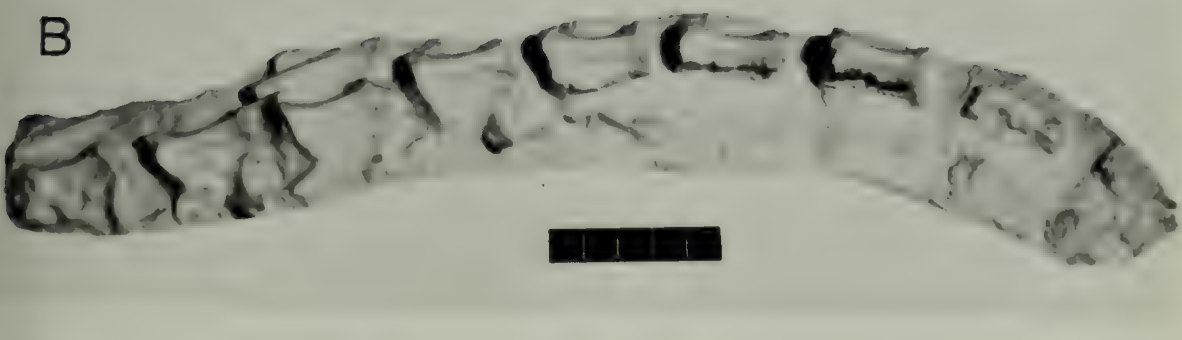


Fig. 2. *Anchisaurus capensis* (Broom). SAM-990. A. Vertebral column in lateral view. Broken edges shown in dashed outline, hatched areas seen in section only. × 0,5. B. Mould of centra of dorsal vertebrae.

tenth vertebra has the only complete neural spine and there is a shallow notch above the postzygapophysis. The ninth and tenth vertebrae are possibly procoelous, with a convexity on the posterior articular surface.

The posterior group of six vertebrae lies slightly to the right of the anterior row, and appears to be in near-natural association with the right ilium. The spine of the most anterior vertebra (the twelfth in the column as preserved) is fairly high and slightly rounded anteriorly; there is only a slight posterior notch above the postzygapophysis. The spine resembles that of the tenth (and eleventh?) vertebra of the anterior row fairly closely. The thirteenth vertebra has a high and narrower spine, posteriorly inclined, and a chevron can be seen extending back and down from below its centrum. The fourteenth and fifteenth vertebrae are similar, as far as can be seen. Remnants of chevrons are seen between the centra of vertebrae fourteen to seventeen.

Identification of vertebral types

Caudal vertebrae are fairly clearly represented by nos. 13 to 17 in the rear series, with narrower, obliquely inclined spines and a series of chevrons. The last two vertebrae (10 and 11) of the anterior row have narrower and possibly higher spines than the preceding ones, and they resemble the first member of the posterior group. From this it can be argued that the tenth, eleventh and twelfth vertebrae of the column as a whole are sacrals, separated by the disintegration of the pelvic girdle. Vertebra 12 is in fairly natural association with the right ilium, and 10 and 11 are close to the ilium of the left side. The left ilium has been displaced sideways and forward relative to the right side, and this could account for the gap in the series. Moreover, no recognizable loose vertebral portions can be identified in the surrounding matrix.

In *Efraasia* (Galton 1973) and *Plateosaurus* (Huene 1926) there are fifteen dorsal vertebrae so, if the above interpretation is correct, the specimen as preserved probably includes dorsal vertebrae 7 to 15, sacral vertebrae 1 to 3, and caudal vertebrae 1 to 5.

Dimensions of the vertebrae, numbered according to their above identification, are given in Table 1.

PELVIC GIRDLE

The pelvic girdle is represented by the right ilium, both ischia, and an incomplete left and almost complete right pubis. The right side of the pelvis (Figs 3, 5) is preserved in almost natural association. The ilium is well preserved, but both pubis and ischium are incomplete distally, and do not make any clear contact with each other. The areas of articulation between ischium, pubis and ilium are imperfectly preserved and could not be determined.

Ilium

The ilium (Figs 3A, 5) of the right side is uncrushed and complete except for a portion of the dorsal crest. It is characterized by long anterior and posterior

TABLE 1.
Dimensions of Vertebrae (mm). *Anchisaurus capensis* (Broom) SAM-990

Vertebra	*Length of centrum ventrally*	*Maximum height*	*Length between pre- and post-zygapophysis*	*Height of spine above post-zygapophysis*	*Length of spine*
7th dorsal . .	27	—	—	—	—
8th dorsal . .	29	—	—	—	—
9th dorsal . .	±30	—	—	—	—
10th dorsal . .	30	—	—	—	—
11th dorsal . .	31	—	—	—	—
12th dorsal . .	31	40	—	13	30
13th dorsal . .	33	42	40	16	32
14th dorsal . .	33	40	48	14	30
15th dorsal . .	32	38	44	13	20
1st sacral . .	31	43	39	19	18
2nd sacral . .	—	—	—	—	—
3rd sacral . .	—	—	35	18	21
1st caudal . .	18	51	34	22	13
2nd–5th caudals .	±18	—	—	—	—

processes, and a pre-acetabular process considerably longer than the post-acetabular process. The anterior process lies slightly external to the more posterior surface of the bone, and extends as far forwards as the anterior edge of the pre-acetabular process. The slender finger-like form of the anterior process (Fig. 10B) is similar to that of *Anchisaurus polyzelus* (Fig. 10A) and *Ammosaurus* (Galton 1971) and in contrast to the small triangle of other prosauropods (Fig. 10C–D).

A prominent pre-acetabular buttress is developed, arising from close above the tip of the pre-acetabular process and flaring out laterally before merging with the body of the ilium at the base of the postacetabular process. The body of the ilium is expanded to a certain extent above the buttress. The postacetabular process is considerably shorter than the pre-acetabular, and takes no part in the formation of the buttress. Above the postacetabular process the ilium is continued posteriorly as a short crest, medial to the base of the posterior process. The maximum length of the ilium is 130 mm.

Pubis

The proximal part of the pubis (Fig. 3A) is incomplete, and the areas of articulation with the ilium and, to a lesser extent, the ischium are not fully preserved. The ventral edge of the bone is deeply notched below the proximal end, and this appears to be a natural condition. Below this embayment, which represents an open obturator foramen, the pubis curves medially and forwards to terminate as a horizontal plate with an average width of 24 mm. The length of the pubis, as preserved, is 145 mm.

For prosauropods an open obturator foramen is described to date only

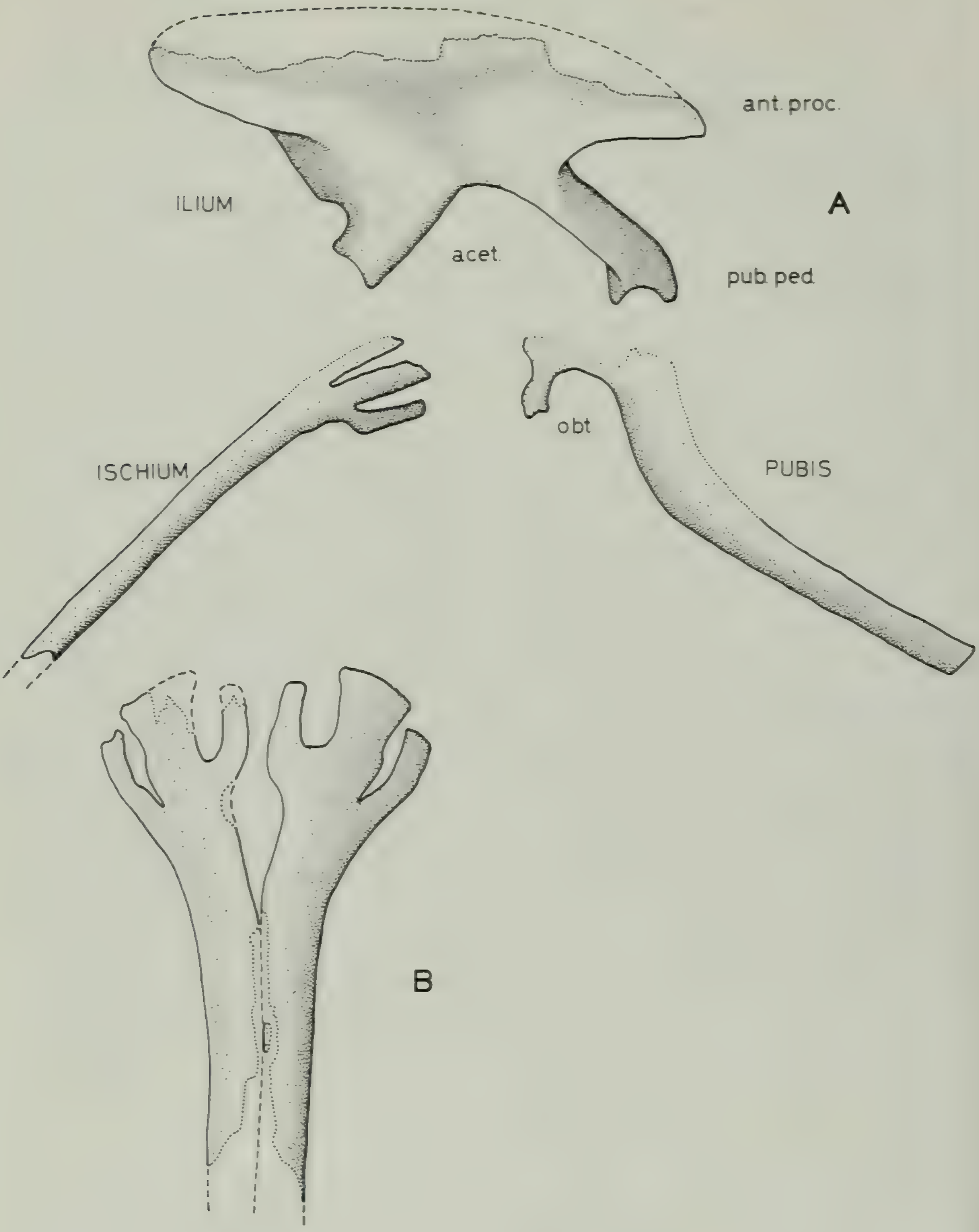


Fig. 3. *Anchisaurus capensis* (Broom), SAM-990. A. Pelvic girdle in right lateral view. B. Ischia in ventral view. × 0,5.

in SAM-990 (Fig. 10H) and *Anchisaurus polyzelus* (Fig. 10G, K); in all other prosauropods it is enclosed ventrally as in *Efraasia* (Fig. 10J, N). A similar open obturator foramen is present in most theropods (for *Allosaurus* and *Ceratosaurus* see Gilmore 1920). Romer (1923) noted that as a result of the more vertical orientation of the archosaurian femur there is a trend amongst archosaurs to reduce that part of the pelvis equivalent to the central portion of the pubo-ischiadic plate of primitive reptiles. The loss of the ventral border of the obturator foramen in *Anchisaurus* (Fig. 10G, H, K) and most therapods probably represents the loss of that portion of the m. pubo-ischio-femoralis externus 2 which originated ventral to the acetabulum in most prosauropods and in all sauropods (see Romer 1923: fig. 2, *Camarasaurus*).

Ischium

Both ischia (Fig. 3), with a preserved length of 136 mm, are present, but are incomplete posteriorly. In each the widened proximal portion is curved outwards and carries two embayments, one above a ventral hook-shaped keel and the other, less clearly defined, lying more dorsally. The proximal portions of the ischia are separated by an ovoid space, but the shafts are closely appressed and form a dorsally open trough.

HIND LIMB

Femur

The femur (Fig. 4A), which is seen in dorsal (anterior) view, is broad and fairly powerful but, with a preserved length of 194 mm, it is incomplete proximally and distally. The proximal end, as shown by what is still preserved, was inclined fairly sharply inwards. Below the proximal end the femur is strongly built and raised to a smooth crest, which runs from proximo-laterally to disto-medially where it merges into the flat distal end. No condyles are preserved, and only an indication of the base of the fourth trochanter can be made out, high in the upper half of the bone.

Fibula

The right fibula (Fig. 4B) lies in its natural position between the femur and the pes and is seen in lateral (external) view. The proximal half is stoutly built and leads to a crest formed in the middle of the bone, directed sideways and forwards. The distal part of the bone is slender and tapers off to the articulation with the pes. Both proximal and distal ends are incomplete and the preserved length of the bone is 176 mm.

Pes

The pes (Figs 4C, 6, 11K) is seen in ventral view, the bones being either eroded or indicated by bone impressions. The calcaneum is incomplete laterally, and probably extended out slightly farther than shown. The astragalus is transversely elongated, with a rounded anterior surface curving back to the

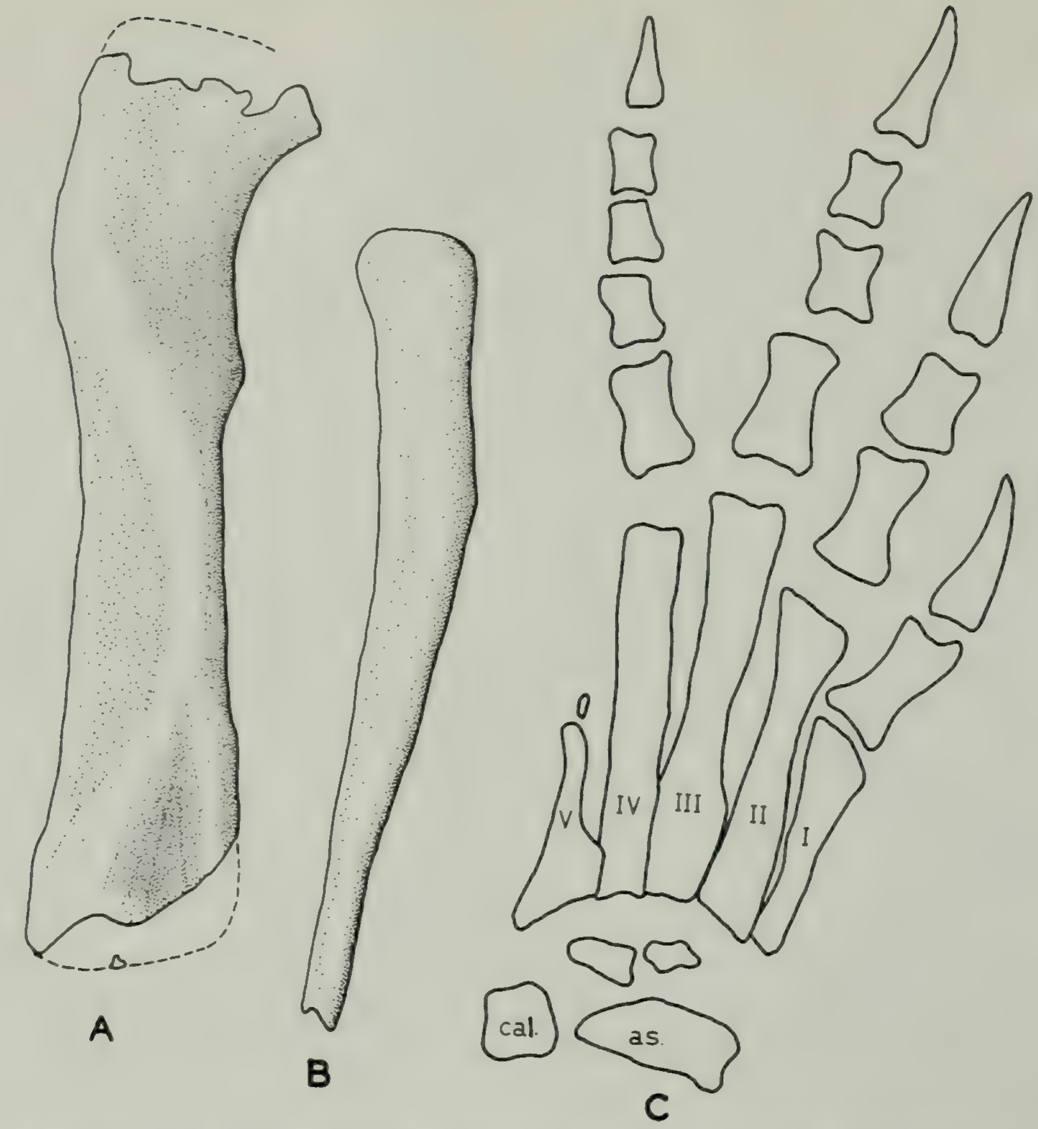


Fig. 4. *Anchisaurus capensis* (Broom), SAM-990. A. Right femur in dorsal (anterior) view. B. Right fibula in lateral view. C. Right pes in ventral view. × 0,5.

narrow lateral corner of the bone. Both calcaneum and astragalus are preserved as impressions, both approximately 15 mm long.

Two small distal tarsal elements are preserved, probably nos 3 and 4. No. 3 is no more than a bony nodule, while 4 is more robust with posterior and medial surfaces at right angles to each other and a convex anterior surface facing metatarsals IV and V. The considerable space between the astragalus and the proximal ends of metatarsals I and II suggests that the two distal tarsals are laterally displaced.

All five metatarsals are preserved, in several cases as somewhat imperfect impressions. There is the usual overlapping of the proximal ends with each metatarsal slightly underlying its medial fellow. Metatarsal V is short and narrow but provided with a strong and wide base. Metatarsal IV is about twice as long and of more or less equal width over its entire length. Metatarsal III is the longest and most robust of the series, while II is slightly shorter than IV. The distal ends of metatarsals III and IV are squarely truncated but metatarsal II terminates in an oblique surface, so that the medial inclination of the row of phalanges seems to be a natural one. This could be true, too, of the short metatarsal I, although this element is incomplete distally.

A small fragment of bone in front of the fifth metatarsal probably represents a vestigial phalanx. The form and degree of preservation of the phalanges are apparent from Figures 4C and 6, and from Table 2.

TABLE 2.
Anchisaurus capensis (Broom), SAM–990. Dimensions of pes (in mm).

Metatarsal length			*Phalanx length (proximal to distal)*				
Metatarsal I	44	Digit I	30	34			
II	76	II	30	22	31		
III	86	III	30	17	14	30	
IV	75	IV	24	16	12	12	21
V	48	V	—				

SLENDER- AND BROAD-FOOTED PROSAUROPODS

When the feet of anchisaurids and plateosaurids are drawn so that digit II of the manus (Fig. 7) or digit III of the pes (Fig. 8) are reduced to unit length then two groups are distinguishable, those with slender feet (Figs 7A, C–D, I, 8D–G, 8I) and those with broad feet (Figs 7B, E–H, J–Q, 8A–C, H, J–S).

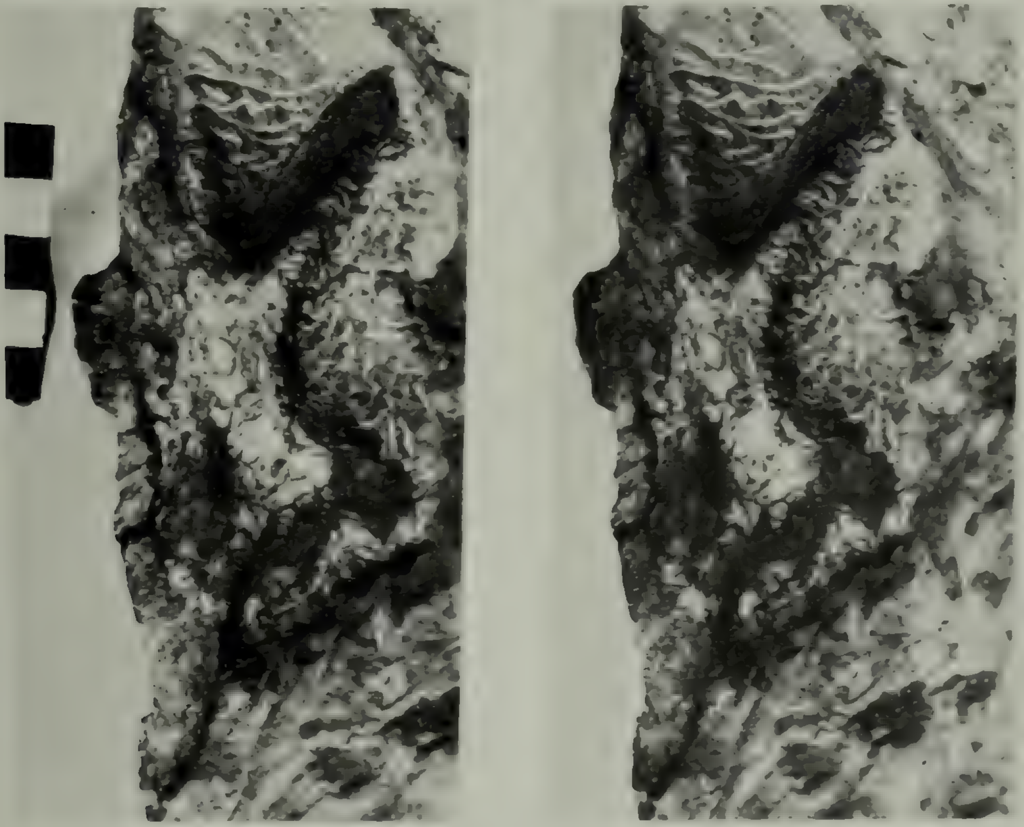


Fig. 5. *Anchisaurus capensis* (Broom), SAM-990. Stereophotograph of right ilium.

The difference is clearest for the manus (digits II to IV) and, where both fore- and hind feet are known, the manus and pes are both slender (Figs 7C, E, I, 8D) or broad (Figs 7B, 8H; 7E, 8K; 7G, 8L; 7J, 8N; 7K, 8O; 7Q, 8Q). The difference between slender and broad feet is not growth related since there are small prosauropods with broad feet (Figs 7B, 8A–C, H). These appear to be juveniles of species that grew much larger (Figs 7B, H, K, 8H, O–P—all *Ammosaurus major*, see Galton 1971) and all the larger prosauropods are broad-footed. The prosauropod families Plateosauridae (Figs 7–8) and Melanorosauridae (see Bonaparte 1972*a*: figs 62, 70; Raath 1972: figs 9f, 10a–b) are all broad-footed, whereas the Anchisauridae as currently classified include both slender and broad-footed forms (Figs 7–8). '*Gyposaurus*' *capensis* (Figs 3C, 5, 7G, 10K) and *Thecodontosaurus antiquus* (Figs 8F, 11G) are both slender-footed species but broad-footed species have been incorrectly referred to both genera.

SYSTEMATIC DISCUSSION

Order SAURISCHIA

Suborder SAUROPODOMORPHA

Infra-order PROSAUROPODA

Family **Anchisauridae** Marsh, 1885

Diagnosis

Smaller forms, skull lightly built, shallow posterior half of lower jaw with articulation in line with tooth row, manus and pes slender.

Genus *Anchisaurus* Marsh, 1885

(includes *Megadactylus* Hitchcock, *Amphisaurus* Marsh, *Gyposaurus* Broom)

Diagnosis

Centra of dorsal vertebrae low, broad bases to neural spines of anterior caudal vertebrae, ilium with long anterior process, pubis with open obturator foramen and a relatively narrow distal part that is not apron-like.

The characters of the skull, neck and manus listed below (p. 133) for *Anchisaurus polyzelus* may also be diagnostic of the genus, but these regions are not known in *A. capensis*.

Anchisaurus polyzelus (Hitchcock, 1865)

Megadactylus polyzelus Hitchcock, 1865: 40, pl. 9 (fig. 6). Cope, 1870: 122A–G, pl. 13 (preocc.).
Amphisaurus polyzelus Marsh, 1882: 84 (preocc.).
Anchisaurus polyzelus Marsh, 1885: 169; 1892: pl. 16 (fig. 3) pl. 17 (fig. 6); 1896: 147, pl. 3 (figs 4–5). Lull, 1915: 119, figs 14–17; 1953: 99, figs 12–14a. Galton, 1971: 782, fig. 7C; 1973: fig. 1F, H, M, O, P, S.
Anchisaurus colurus Marsh, 1891: 267; 1892: 543, pl. 15, 16 (figs 1, 2); 1893: 169, pl. 6; 1896: 148, pl. 2 (figs 1–3), pl. 3 (figs 1, 2), pl. 4. Huene, 1906: 6, figs 1–6, pls 1–3; 1914*b*: 69, figs 1–11; Lull, 1912: 414, figs 2–3; 1915: 130, figs 18–21, pls 4, 10.
Thecodontosaurus polyzelus Huene, 1906: 19, figs 10, 10a; 1914*b*: 75, figs 23–24; 1932: 116.
Yaleosaurus colurus Huene, 1932: 119, pl. 14 (fig. 1), pl. 54 (fig. 3). Lull, 1953: 107, figs 15–18, pl. 4.

Types

Incomplete skeleton (AM 41/109) from Longmeadow Sandstone, upper part of Newark Series (Upper Triassic) of Springfield, Massachusetts, U.S.A. (*A. polyzelus*). Almost complete skeleton (YPM 1883) from Portland beds, upper part of Newark Series near Manchester, Conn., U.S.A. (*A. colurus*).

Diagnosis

± 9 maxillary teeth, 16 dentary teeth, basipterygoid processes very small, cervical vertebrae elongate, metacarpal I broad, digits II and III of manus subequal in length, ungual I of pes smaller than ungual II.

Discussion

Megadactylus Hitchcock being preoccupied, Marsh (1882) replaced it with *Amphisaurus* (also preoccupied) and then *Anchisaurus* (Family Anchisauridae also proposed). Huene (1906) referred the material of *Megadactylus polyzelus* Hitchcock to *Thecodontosaurus* as *T. polyzelus* (Hitchcock) and used the Family Thecodontosauridae (originally proposed by Lydekker, 1890: 246) to replace Anchisauridae. Marsh (1891) made YPM 1883 the holotype of a new species of *Anchisaurus*, *A. colurus*, but he did not indicate how it differed from *A. polyzelus* (AM 41/109). Huene (1906) suggested that *Anchisaurus polyzelus* resembled *Thecodontosaurus* and differed from *Anchisaurus colurus* in several features, discussed here together with others noted later by Huene (1907–08, 1932) (for full discussion see Galton, in press):

1. *Shortness of cervical vertebrae.* Huene (1932) noted that AM 41/109 resembled *Thecodontosaurus* (Fig. 11A) in the shortness of the anterior cervical vertebrae, which are elongate in YPM 1883 (Figs 9H, 11B). However, this comparison was based on misidentification of part of the neural arch of a dorsal vertebra (Galton in press, fig. 3a–c) as a cervical vertebra (Huene 1914*b*: fig. 23a).

2. *Shortness of dorsal vertebrae.* Huene (1906) originally noted that AM 41/109 differed from *Thecodontosaurus* and resembled YPM 1883 in having very elongate dorsal vertebrae. Later Huene (1914*b*) figured an extremely short centrum of AM 41/109 as that of a dorsal vertebra. Although not stated, this implied that the dorsal vertebrae of AM 41/109 are extremely short as in *Thecodontosaurus*. The isolated centrum figured by Huene (1914*b*) could not be located but judging from the proportions it was probably part of an anterior caudal vertebra. The proportions of an isolated neural arch (Galton in press, fig. 3a–c) and of a centrum (Galton in press, fig. 5c) show that the dorsal vertebrae of AM 41/109 were probably elongate (i.e. the centra were low) as in YPM 1883 (Fig. 9K).

3. *Slenderness of neural spines of anterior caudal vertebrae.* This comparison by Huene (1906) was based on misleading figures given by Cope (1870) and Marsh (1893, 1895, 1896). Cope (1870: pl. 8 (fig. 7): see Lull 1953:

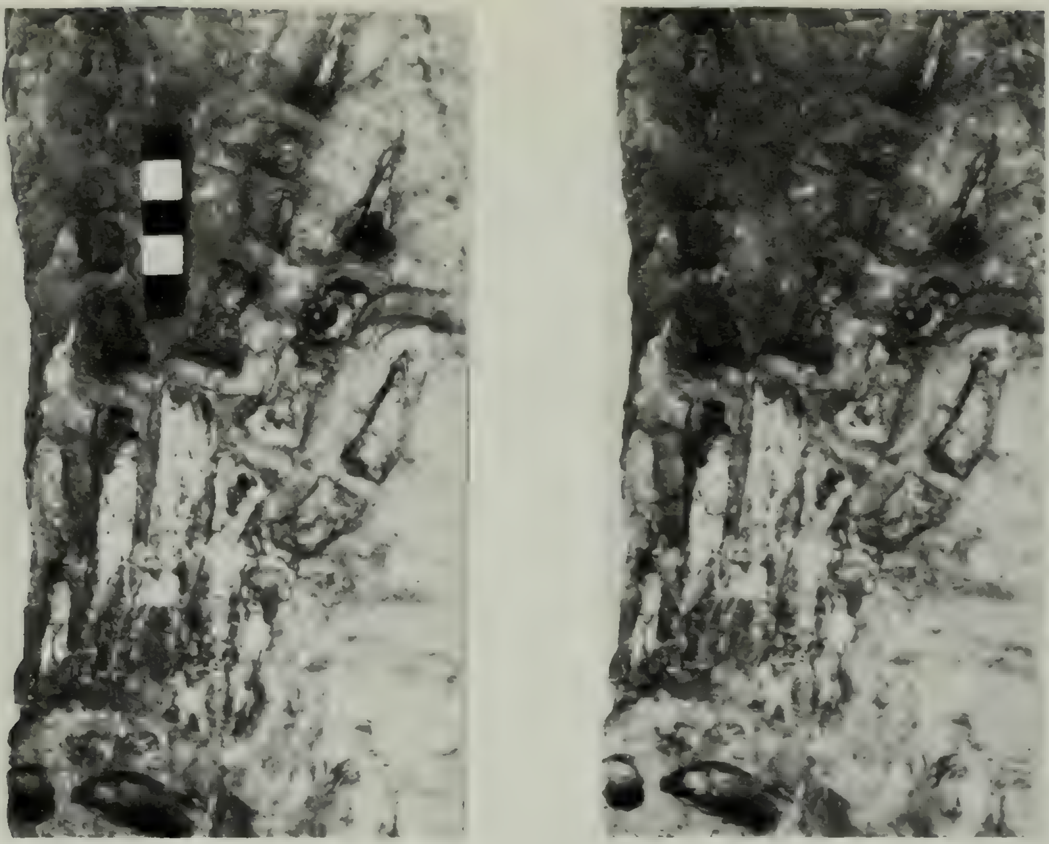


Fig. 6. *Anchisaurus capensis* (Broom), SAM-990. Stereophotograph of right pes in ventral view.

fig. 12a) did not indicate that the neural spines of the anterior caudal vertebrae of AM 41/109 were damaged and incomplete (Fig. 9P); originally the neural spines were broader and not as narrow as in the vertebrae referred to *Thecodontosaurus* (Fig. 9S) by Huene (1907–08: pl. 77 (fig. 4); 1914*b*: fig. 40).

Most of the supposed differences between AM 41/109 and YPM 1883 were either the result of misinterpretation (1–3 above, different position of fourth trochanter of femur) or the result of differences in preservation (form of radius, metacarpals, tibia, fibula: see Galton in press). YPM 1883 does differ from AM 41/109 in having a proportionally long centrum to the last dorsal vertebra (but this might be sacral vertebra 3) and a proportionally smaller manus with a less trenchant first ungual phalanx (Fig. 7A, C). However, these differences probably represent individual variations within a species because individuals of the ornithopod dinosaur *Hypsilophodon foxii* show a much wider range of morphological variation (see Galton 1974). YPM 1883 should be referred to *Anchisaurus polyzelus* because, on the basis of available material, it cannot be distinguished from AM 41/109 by any characters of taxonomic significance and, in addition, AM 41/109 does not show any unique resemblance to *Thecodontosaurus*. Consequently, *Anchisaurus colurus* Marsh is a junior synonym of *Anchisaurus polyzelus* (Hitchcock) and, as *A. colurus* is the type species of the

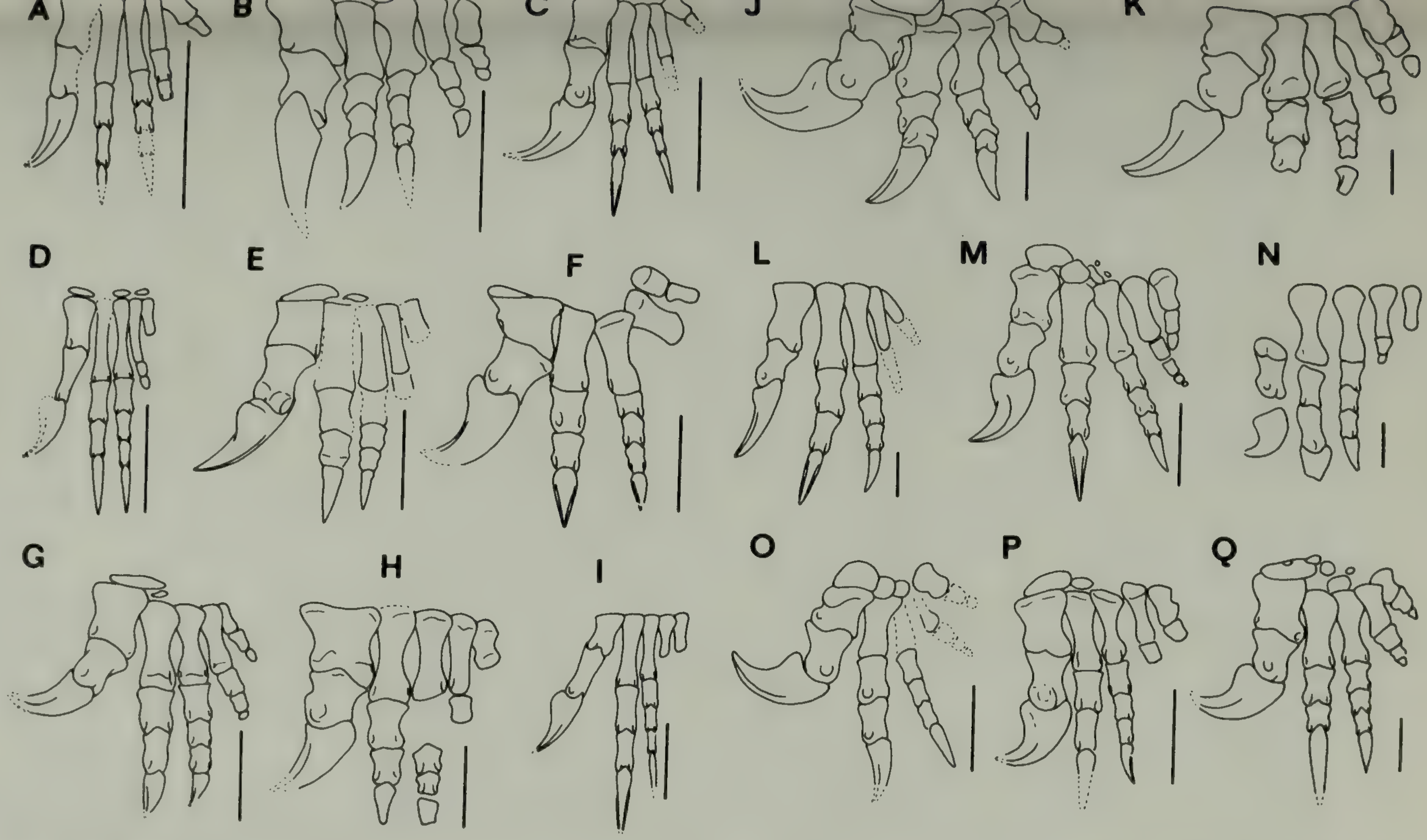


Fig. 7. Comparison of the manus of prosauropods, either right in dorsal view or left in ventral view (E), all drawn to digit II unit length, scale = 5 cm. These genera are divided by Romer (1966) between the families Anchisauridae (A–D, F, J, O–Q) and Plateosauridae (H, K–N). A. *Anchisaurus polyzelus* AM 41/109. B. *Lufengosaurus huenei*, figured as *Gyposaurus sinensis* by Young (1941). C. *Anchisaurus polyzelus*, YPM 1883. D. *Thecodontosaurus antiquus*, YPM 2195. E. *Ammosaurus* cf. *major*, Galton (1971). F. *Massospondylus harriesi*, figured as *M. browni* by Van Hoepen (1920*b*). H. *Lufengosaurus huenei*, figured as *Yunnanosaurus huangi* by Young (1942). I. *Efraasia diagnostica*, SMNS 12667. J. *Massospondylus harriesi*, from Broom (1911). K. *Lufengosaurus huenei*, figured as *L. magnus* by Young (1947). L. *Plateosaurus erlenbergiensis*, after Galton (1971). M. *Plateosaurus* sp., figured as *Pachysaurus ajax* by Huene (1932). N. *Plateosaurus* sp., figured as *Teratosaurus minor* by Huene (1907–08). O. *Aetonyx palustris*, from Broom (1911). P. *Aetonyx palustris*, AMNH 5624. Q. *Gryponyx africanus*, from Broom (1911).

genus *Yaleosaurus* (Huene 1932: 122), *Yaleosaurus* is a junior synonym of *Anchisaurus* Marsh, 1885.

Anchisaurus capensis (Broom, 1911)

Hortalotarsus skirtopodus (*non* Seeley, 1894) Broom, 1906: 201, pl. 3.
Gyposaurus capensis Broom, 1911: 293.

Type

Partial skeleton (SAM-990) from the Cave Sandstone, Stormberg Series (Upper Triassic) of Ladybrand, Orange Free State, South Africa.

Diagnosis

Ungual 1 largest on pes.

Discussion

Because of its nature, SAM-990 can be distinguished from *Anchisaurus polyzelus* (YPM 1883) only by the relative size of ungual 1 of the pes—large in SAM-990 and small in YPM 1883. *Anchisaurus capensis* (Broom) is distinguishable from all prosauropods other than *A. polyzelus* (Hitchcock) by the following combination of characters:

1. Centra of posterior dorsal vertebrae (about the tenth) are proportionally low so that the ratio of central length to height ($\frac{L}{H}$) is 2,1 (Figs 2, 9L).
2. Anterior process of ilium is elongate (Figs 3, 5, 10B).
3. Subacetabular part of pubis is emarginated ventrally so that the obturator foramen is open (Figs 3, 10H).
4. The pes is slender (Figs 4C, 6C, 11K).
5. Broad bases to neural spines of anterior caudal vertebrae (Figs 2, 9Q).

The form of these elements in the species of Anchisauridae is summarized in Table 3 to facilitate comparisons. The systematic position of other species incorrectly referred to '*Gyposaurus*' are discussed below (pp. 141, 143, 147).

TABLE 3.
Comparison of species attributed to '*Gyposaurus*' with other anchisaurids.

	Dorsal Centra: length/ height	*Neural spine of anterior caudal*	*Anterior process of ilium*	*Proximal pubis/ obturator foramen*	*Pes*
'*Gyposaurus*' *capensis* . .	2,1	wide	long	shallow/open	slender
'*Gyposaurus*' *erectus* . .	1,4	wide	short	deep/closed	broad
'*Gyposaurus*' *sinensis* . .	1,1	—	short	deep/closed	broad
Anchisaurus polyzelus .	2,1	wide	long	shallow/open	slender
Thecodontosaurus antiquus .	1,7	narrow	short	—	slender
Efraasia diagnostica . .	2,5	narrow	short	deep/closed	slender

Genus *Efraasia* Galton, 1973

Diagnosis

Basipterygoid processes of medium length, cervical vertebrae elongate, centra of dorsal vertebrae low, narrow bases to neural spines of anterior caudal vertebrae, slender metacarpal I, digit II of the manus robust and appreciably longer than digit III, ilium with short triangular anterior process, pubis with closed obturator foramen with an apron-like distal part, ungual 1 largest in pes.

Efraasia diagnostica (Huene)

Thecodontosaurus diagnosticus Fraas, 1913: 1098 (*nomen nudum*).
Palaeosaurus (?) *diagnosticus* Huene, 1932: 52, 73, figs 1, 2, 7–8, pls 4–6.
Palaeosauriscus diagnosticus Charig, 1967: 712.
Efraasia diagnostica Galton, 1973: 247, figs 1A–E, 2–15, 16A, 17C–D.

Syntypes

An almost complete skeleton (SMNS 12667) (Berckhemer 1938) together with additional material (SMNS 12668) from the Stubensandstein (Upper Triassic) of Pfaffenhofen, Württemberg, West Germany (see Galton 1973).

Diagnosis

As for genus.

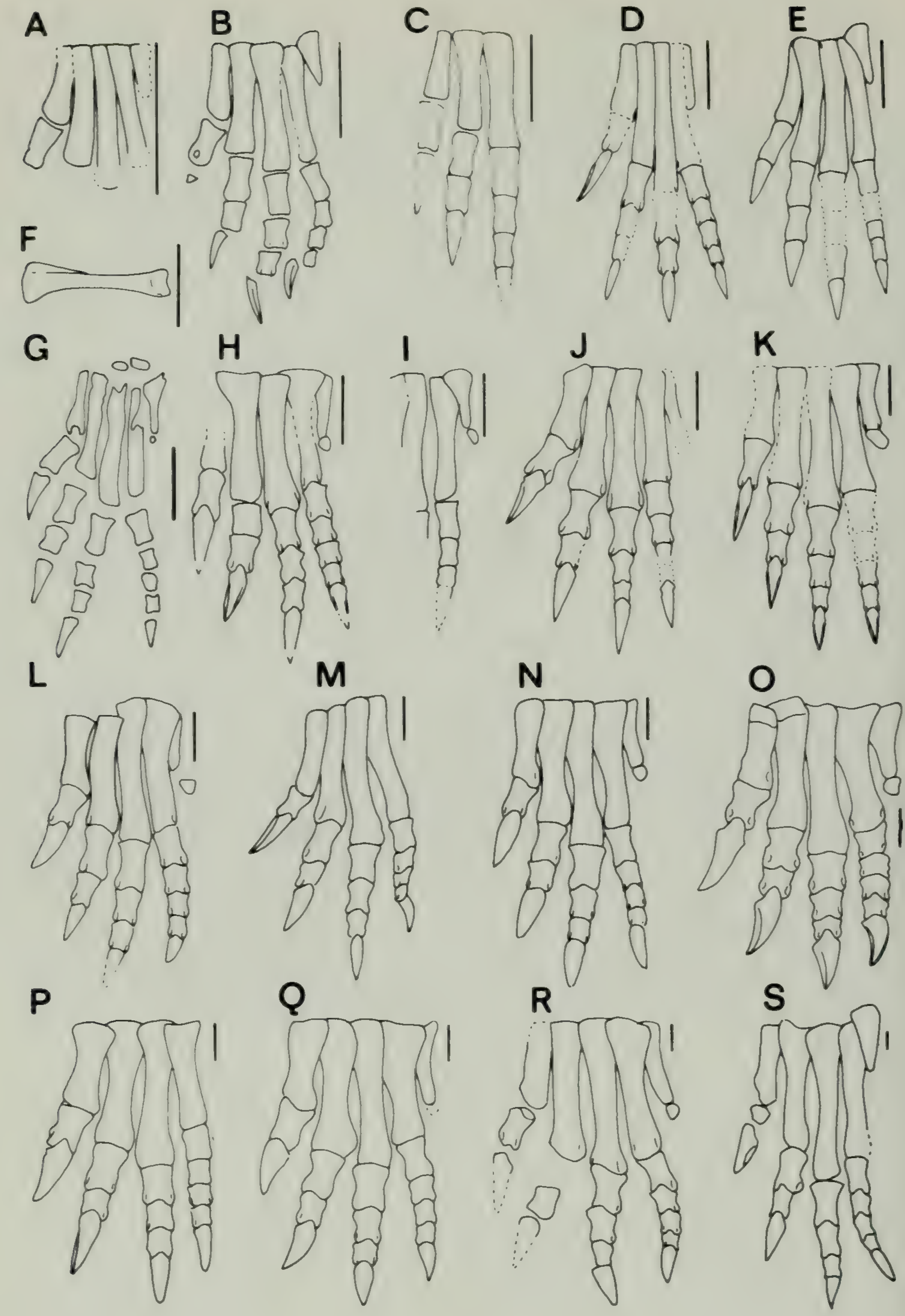
Discussion

As shown by the manus (Fig. 7I) and the pes (Figs 8D, 11M), *Efraasia diagnostica* undoubtedly represents a slender-footed prosauropod. Apart from that of *Anchisaurus polyzelus* (YPM 1883, Fig. 12B; Huene 1906: pl. 1), this is the only reasonably complete and well-preserved skeleton (Fig. 12A; Berckhemer 1938) of a slender-footed prosauropod described to date. *Efraasia diagnostica* (Figs 7I, 8D, 9I, M, 10D, J, N, 11M) resembles *Anchisaurus capensis* in several features (Table 3) but differs in three important respects, viz. the ilium has a short triangular anterior process (Fig. 10D), the subacetabular part of the pubis is deep with a complete obturator foramen (Fig. 10J, N), and the bases of the neural spines of the anterior caudal vertebrae are narrow (Fig. 9R).

Genus *Thecodontosaurus* Riley & Stutchbury, 1836

Diagnosis

At least 21 dentary teeth (in holotype, Fig. 9B); from referred specimens without teeth diagnosis tentatively expanded as follows: elongate basipterygoid processes, cervical vertebrae proportionally short compared with other anchisaurids, high centra to dorsal vertebrae, narrow base to neural spines of anterior and caudal vertebrae, high placed deltopectoral crest on proximal third of humerus, manus with slender metacarpal I and digits II and III subequal in length, short triangular anterior process to ilium.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Thecodontosaurus antiquus Morris

Thecodontosaurus Riley & Stutchbury, 1836: 398; 1840: 352, pl. 29 (figs 1–2).
Thecodontosaurus antiquus Morris, 1843: 211.

Type

Incomplete dentary with teeth from the Magnesian Conglomerate (Upper Triassic) near Bristol, England.

Diagnosis

As for genus.

Discussion

Riley & Stutchbury (1836, 1840) did not give a specific name for *Thecodontosaurus* and this oversight was rectified by the proposal of *T. antiquus* Morris, 1843.

Thecodontosaurus was the first genus of prosauropod to be described so it is unfortunate that there is no articulated association between teeth of the type and the postcranial material referred to the genus by Seeley (1895*a*) and Huene (1907–8, 1914*b*). Indeed, the only articulated bones referred to *Thecodontosaurus* are a few short sequences of vertebrae (Huene 1907–8: figs 214, 218–220) and a fore limb with scapula, cervical vertebra and dorsal ribs (Fig. 11A–G). The description and skeletal reconstruction of *Thecodontosaurus antiquus* given by Huene (1932: 116, pl. 54 (fig. 1)) are based on many specimens. However, the postcranial remains from Bristol indicate the presence of a slender-footed prosauropod (Fig. 11A–G) and it is reasonable to refer this material to *Thecodontosaurus antiquus*. Species of *Thecodontosaurus* from other parts of the world (see next section and pp. 145, 147, 152, 153) are incorrectly referred to this genus.

Fig. 8. Comparison of the pes in various prosauropods, either right in dorsal view or left in ventral view (A, C, E, G, I,), all drawn to digit III unit length, scale lines represent 5 cm. These genera are divided by Romer (1966) between the families Anchisauridae (B, C, E–I, L, N, Q) and Plateosauridae (M, O, P, R, S). A. *Ammosaurus major*, YPM 209. B. *Aristosaurus erectus*, from Van Hoepen (1920*a*). C. *Thecodontosaurus browni*, from Huene (1932). D. *Efraasia diagnostica*, SMNS 12668. E. *Anchisaurus polyzelus*, YPM 1883. F. *Thecodontosaurus antiquus*, metatarsal III, from Huene (1907–08). G. *Anchisaurus capensis*, SAM-990. H. *Lufengosaurus huenei*, figured as *Gyposaurus sinensis* by Young (1941). I. *Hortalotarsus skirtopodus*, figured as *Thecodontosaurus skirtopodus* by Huene (1906). J. *Ammosaurus major*, YPM 208. K. *Ammosaurus* cf. *major*, from Galton (1971). L. *Massospondylus harriesi*, figured as *M. browni* by Van Hoepen (1920*b*). M. *Plateosaurus gracilis*, from Berckhemer (1938). N. *Massospondylus harriesi*, from Broom (1911). O. *Lufengosaurus huenei*, figured as *Yunnanosaurus magnus* by Young (1947). P. *Lufengosaurus huenei*, figured as *Yunnanosaurus robustus* by Young (1951). Q. *Gryponyx africanus*, from Broom (1911). R. *Plateosaurus robustus*, from Huene (1932). S. *Plateosaurus* sp., figured as *Pachysaurus wetzelianus* by Huene (1932).

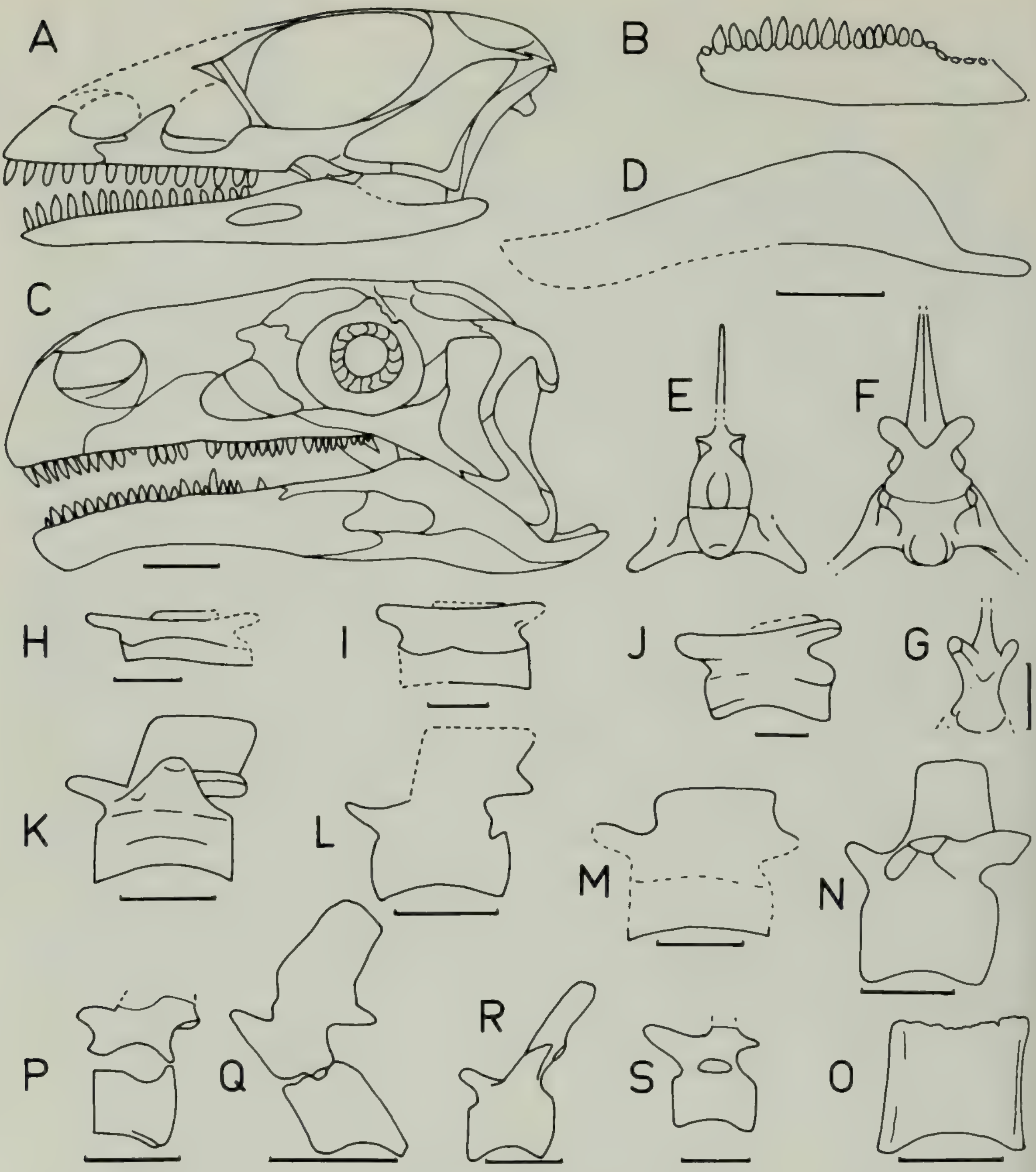

Fig. 9. Comparison of skulls and vertebrae of prosauropods, scale = 2,5 cm, A, B, D–F × 0,5. A. Skull of *Anchisaurus polyzelus*, YPM 1883, lateral view. B. *Thecodontosaurus antiquus*, left partial dentary in lateral view, from Riley & Stutchbury (1840). C. Skull of *Plateosaurus* in lateral view, from Romer (1966). D. *Massospondylus harriesi*, left partial lower jaw in lateral view, from Haughton (1924). E–G. Braincases in ventral view: E. *Anchisaurus polyzelus*, YPM 1883. F. *Thecodontosaurus antiquus*, YPM 2192. G. *Efraasia diagnostica* basisphenoid, SMNS 12667. H–J. Third cervical vertebra in lateral view: H. *Anchisaurus polyzelus*, YPM 1883. I. *Efraasia diagnostica*, SMNS 12667. J. *Lufengosaurus huenei*, figured as *Gyposaurus sinensis* by Young (1941). K–O. dorsal vertebrae (tenth to twelfth) in lateral view: K. *Anchisaurus polyzelus*, YPM 1883. L. *Anchisaurus capensis*, SAM-990. M. *Efraasia diagnostica*, SMNS 12667. S. *Thecodontosaurus antiquus*, from Huene (1907–08).

Anchisauridae *nomina dubia*

Hortalotarsus skirtopodus Seeley, 1894

Hortalotarsus skirtopodus Seeley, 1894: 411, figs 1–3.
Thecodontosaurus skirtopodus Huene, 1906: 44, figs 72–78, pls 13, 14. Haughton, 1924: 370. Huene, 1932: 117. Haughton & Brink, 1954: 35.
Gyposaurus skirtopodus Charig, 1967: 712.

Type

Incomplete hind limb in the Albany Museum, from the Cave Sandstone, Stormberg Series, of Barkly East Division, Cape Province, South Africa.

Discussion

The assignment of *Hortalotarsus skirtopodus* to *Thecodontosaurus* by Huene (1906) was based in part on the characters of isolated bones found at localities different from that of the type specimen. The pes of the type (Fig. 8I) is obviously that of a slender-footed prosauropod, and Huene (1906) could not distinguish it from the pes of *Thecodontosaurus*. However, this pes (Fig. 8I) is also indistinguishable from those of *Anchisaurus capensis* (Fig. 11K), *Anchisaurus polyzelus* (Fig. 11L) and *Efraasia diagnostica* (Fig. 11M). This specimen is generically and specifically indeterminate so *Hortalotarsus skirtopodus* Seeley is a *nomen dubium*.

Thecodontosaurus browni (Seeley, 1895*b*)

Massospondylus browni Seeley, 1895*b*: 118, figs 13–14.
Thecodontosaurus browni Huene, 1906: 141, pl. 12 (figs 7–8); 1932: 118. Broom, 1911: 293. Haughton, 1924: 370.

Type

Limb bones (BMNH R3302) from the Red Beds, Stormberg Series of Telle River, Herschel, Cape Province, South Africa.

Discussion

Seeley (1895*b*) noted that the proportions of the phalanges of the pes are very similar to those of *Hortalotarsus* (Fig. 8H) so this is probably another generically and specifically indeterminate specimen of a slender-footed prosauropod.

Thecodontosaurus minor Haughton, 1918

Thecodontosaurus minor Haughton, 1918: 468; 1924: 376, fig. 21.
Thecodontosaurus browni: Huene, 1932: 118.

Type

Left tibia, a cervical vertebra and a portion of a left ilium (SAM-3451) from the Red Beds, Stormberg Series, from road-cutting at Naude's Nek, Pitsing, Maclear District, Cape Province, South Africa.

Discussion

The tibia is slender so this may be a slender-footed prosauropod but, on

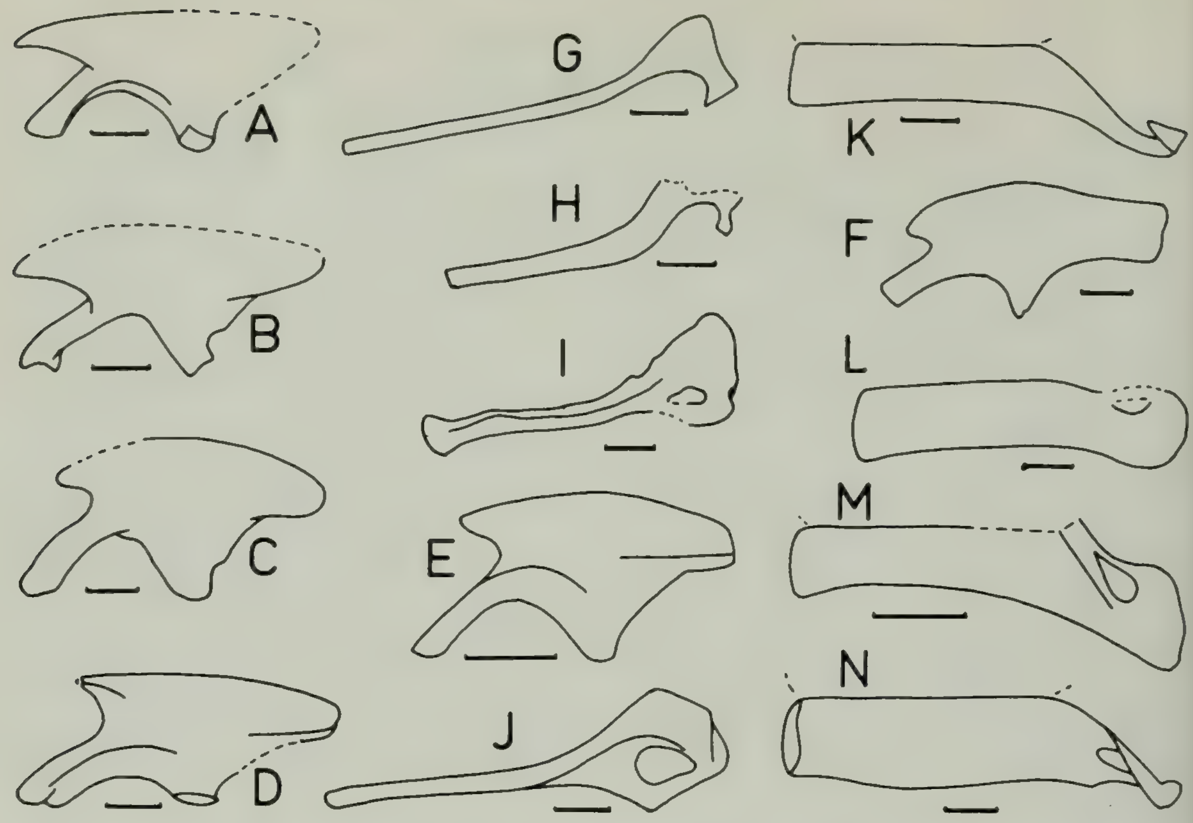

Fig. 10. Comparison of ilium and pubis of prosauropods. Scale - 2,5 cm. A–F. Lateral view of left ilium: A. *Anchisaurus polyzelus*, YPM 1883. B. *Anchisaurus capensis*, SAM-990. C. *Lufengosaurus huenei*, figured as *Gyposaurus sinensis* by Young (1941). D. *Efraasia diagnostica*, SMNS 12667. E. *Aristosaurus erectus*, fromVan Hoepen (1920*a*). F. *Thecodontosaurus antiquus*, from Huene (1907–08). G–J. lateral view of left pubis: G. as A. H as B. I as C. J as D. K–N. Ventral view of right pubis (L, M) or dorsal view of left pubis (K, N): K as A, G. L as C, I. M as E. N as D, J.

the basis of available material, this specimen is a generically and specifically indeterminate prosauropod and *Thecodontosaurus minor* is a *nomen dubium*.

Thecodontosaurus macgilivrayi (Seeley)

Agrosaurus macgilivrayi Seeley, 1891: 161, figs 1–6.
Thecodontosaurus macgilivrayi Huene, 1906: 147, figs 86–90; 1932: 52.

Type

Tibiae, radius, an ungual and tooth (BMNH 49984) from York Peninsula, Queensland, Australia.

Discussion

Huene (1932: 52) subsequently referred *Agrosaurus macgilivrayi* to the Theropoda (Coelurosauria) as do Romer (1956, 1966), Steel (1970) and White (1973). However, the latero-distal surface of the tibia is notched (Fig. 11H–J) (Huene 1906: fig. 86a, d–e) to receive the central ascending process of the astragalus in typical prosauropod fashion. This material undoubtedly represents a prosauropod but is generically and specifically indeterminate, so *Agrosaurus macgilivrayi* is a *nomen dubium*; it may represent a slender-footed prosauropod.

PROSAUROPOD SPECIES INCORRECTLY ASSIGNED TO ANCHISAURIDAE

Family **Plateosauridae** Marsh, 1895

Diagnosis

Larger forms, skull massively built, deep posterior half to lower jaw with articulation offset ventral to line of tooth row, manus and pes broad.

Ammosaurus major Marsh, 1889

Anchisaurus major Marsh, 1889: 331, fig. 1.
Ammosaurus major Marsh, 1891: 267; 1892: 545, pl. 16 (fig. 4), pl. 17 (fig. 3); 1896: 150, pl. 3 (figs 3, 6). Huene, 1906: 15, pls 5–9; 1907–08: 303–04, figs 297–298; 1914*a*: 13; 1914*b*: 74, figs 20–22; 1932: 26. Lull, 1915: 148, figs 24–25; 1953: 123, figs 19–20. Galton, 1971: 786, figs 9, 11A.
Anchisaurus solus Marsh, 1892: 545; 1896: 149. Huene, 1914*b*: 72, figs 12–19. Lull, 1915: 144, figs 22–23; 1953: 120.
Anchisaurus (?) *solus* Huene, 1906: 14, pl. 4.
Ammosaurus solus Huene, 1932: 27, pl. 49 (fig. 1).

Type

Pelvis and hind limbs (YPM 208) from the Portland Beds, upper part of Newark Series near Manchester, Connecticut, U.S.A. (*Ammosaurus major*). Almost complete skeleton (YPM 209) from the same locality and horizon (*Anchisaurus solus*).

Discussion

Ammosaurus has long been regarded as a primitive theropod dinosaur but it is considered as an anchisaurid by Steel (1970) and by Galton (1971), who provides a detailed discussion of the taxonomic position of this genus (Galton in press). The pes of the holotype (Fig. 8J) and of the referred specimens (Fig. 8A, K) plus a referred manus (Fig. 7E) are of the broad type. *Ammosaurus* is a broad-footed prosauropod characterized by the following combination of characters: centra of dorsal vertebrae low, slender sacral rib 3, elongate anterior process to ilium, subacetabular part of the ischium emarginated ventrally (Galton, in press).

Aristosaurus erectus van Hoepen, 1920*a*

Aristosaurus erectus van Hoepen, 1920*a*: 82, figs 1–6, pls 9–10. Haughton 1924: 379. Haughton & Brink, 1954: 33.
Gyposaurus capensis Huene, 1932: 123, pl. 54 (fig. 2).
Gyposaurus erectus Charig, 1967: 712. Steel, 1970: 49.

Type

An almost complete skeleton as slab and counterpart (TM 130) from the Cave Sandstone, Stormberg Series, near Roosendal, Senekal District, Orange Free State, South Africa.

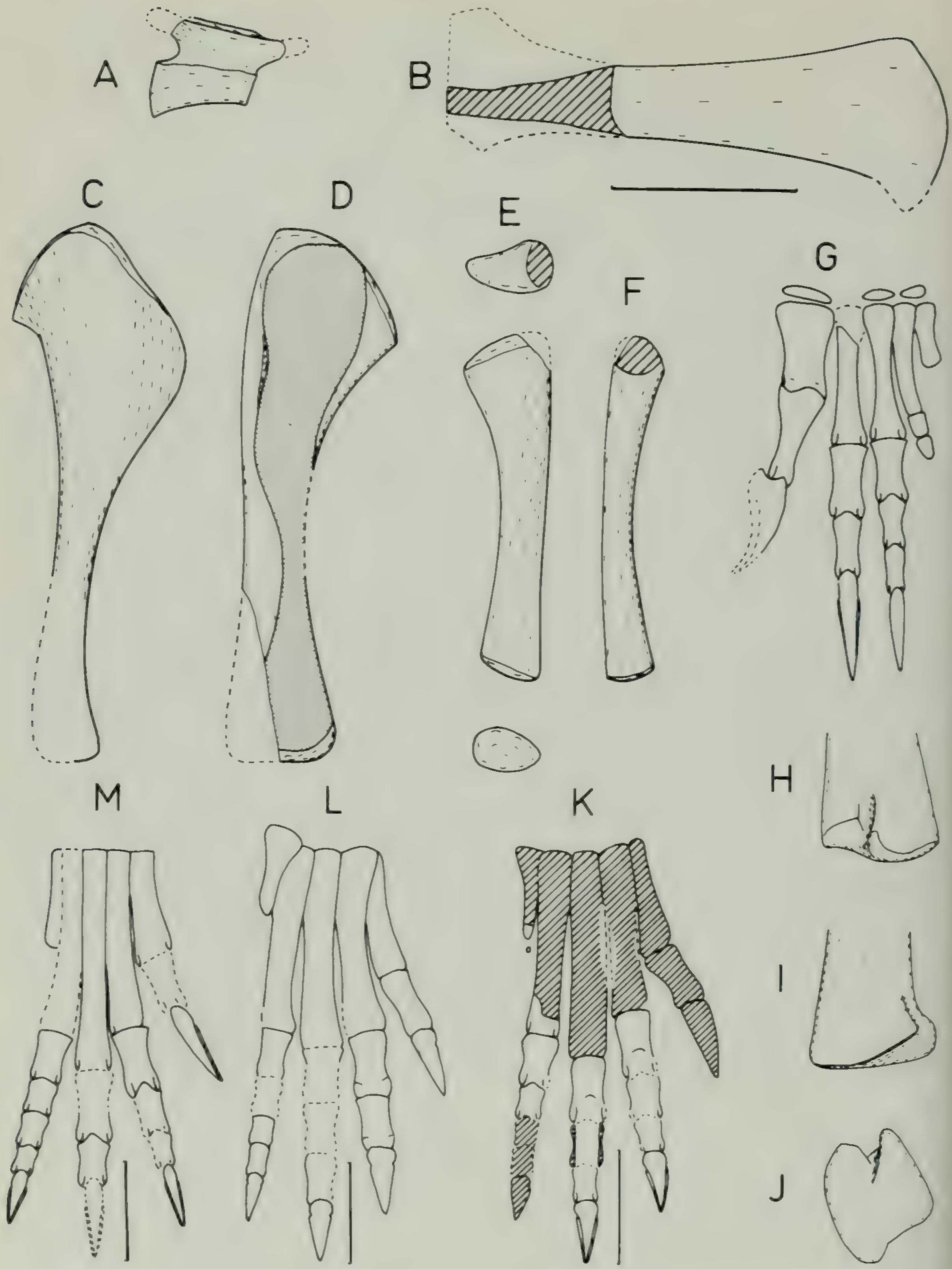

Fig. 11. *Thecodontosaurus*, *Agrosaurus* and comparisons of the anchisaurid pes. Scale = 5 cm, A–J = × 0,45. A–G. *Thecodontosaurus antiquus*, YPM 2195, from Durdham Down, Bristol, England. Matrix indicated by stipple, broken bone by diagonal shading: A. Right side of anterior cervical vertebra. B. Right scapula in lateral view. C. Left humerus in medial view. D. As C, in anterior view. E. Left ulna in proximal, lateral and distal views. F. Left radius in lateral view. G. Left manus in lateral or dorsal view. H–J. *Agrosaurus macgillivrayi*, distal end of left tibia in lateral view (H), anterior view (I), and distal view (J), all from Huene (1906). K–M. Anchisaurid pes, drawn to digit III unit length: K. *Anchisaurus capensis*, SAM-990, compare with Fig. 5. L. *Anchisaurus polyzelus*, YPM 1883. M. *Efraasia diagnostica*, SMNS 12668.

Discussion

Romer (1956, 1966), Charig (1967), Steel (1970) and White (1973) follow Huene (1932, 1956) in regarding *Aristosaurus* as a junior synonym for *Gyposaurus* but this is unlikely because, in contrast to the situation in *Gyposaurus capensis* (Table 3):

1. In photographs of the skeleton of *Aristosaurus erectus* in Van Hoepen (1920*a*: pls 9–10) and in the reconstruction (Fig. 12D) given by Huene (1932) the dorsal vertebrae are proportionally higher with a central length to height ratio of about 1,4 for dorsal 10.
2. The anterior process of the ilium is short (Fig. 10E).
3. The obturator foramen of the pubis is closed ventrally (Fig 10M).
4. The hind feet of *Aristosaurus erectus* appear to be of the broad type.

There is no reason why *Aristosaurus erectus* should be referred to the genus *Anchisaurus*. *Aristosaurus erectus* appears to be a valid taxon of broad-footed prosauropod, but further preparation and illustration of the holotype is needed.

Genus *Massospondylus* Owen, 1854

(includes *Leptospondylus* Owen, *Pachyspondylus* Owen, *Aetonyx* Broom, *Gryponyx* Broom, *Dromicosaurus* Van Hoepen)

Massospondylus carinatus Owen, 1854

Massospondylus carinatus Owen, 1854: 97. Seeley, 1895*b*: 102, figs 1–12. Huene, 1906: 36, figs 43–70, pls 13–16. Broom, 1911: 241. Haughton, 1924: 383. Huene, 1932: 124.
Leptospondylus capensis Owen, 1854: 97.
Pachyspondylus orpenii Owen, 1854: 97.

Type

Isolated bones from the Red Beds, Stormberg Series of Beaucherf, Harrismith, Orange Free State, South Africa. The holotype in the Museum of the Royal College of Surgeons in London was destroyed during World War II but casts of this material are in the National Museum of Southern Rhodesia, Bulawayo (J. Attridge, pers. comm.).

Massospondylus harriesi Broom, 1911

Massospondylus harriesi Broom, 1911: 299, pls 15–17. Haughton, 1924: 384, figs 21–29. Huene, 1932: 125.
Massospondylus browni (*non* Seeley, 1895*b*): Van Hoepen 1920*b*: 118, pls 17–22.
Aetonyx palustris Broom, 1911: 304, figs 20–23. Haughton, 1924: 404, fig. 30. Huene, 1932: 91.
Gryponyx africanus Broom, 1911: 294, figs 1–9. Haughton, 1924: 417, figs 36–38. Huene, 1932: 88, pl. 7 (figs 1–4).
Gryponyx taylori Haughton, 1924: 420, fig. 39. Huene, 1932: 90.
Dromicosaurus gracilis Van Hoepen, 1920*b*: 103, figs 8–21, pls 13–16. Haughton, 1924: 405.
Thecodontosaurus dubius Haughton, 1924: 377.

Types

Massospondylus harriesi: Bones of the fore limb (SAM-3394) from the top of the Red Beds, Stormberg Series of Foutanie, Fouriesburg, Orange Free State, South Africa.

Aetonyx palustris: Partial skeleton (SAM-2768, 2769, 2770) from the top of the Red Beds (but listed as from Cave Sandstone by C. E. Gow *in* Anderson & Anderson 1970), Stormberg Series from Foutanie, Fouriesburg, Orange Free State, South Africa.

Gryponyx africanus: Pelvis and hind limb, right and left manus, vertebrae (SAM-3357–9) from the top of the Red Beds (but listed as from the Cave Sandstone by C. E. Gow *in* Anderson & Anderson 1970), Stormberg Series of Foutanie, Fouriesburg, Orange Free State, South Africa.

Gryponyx taylori: Pelvic girdle and sacral vertebrae (SAM-3453) from the top of the Red Beds (but listed as from Cave Sandstone by C. E. Gow *in* Anderson & Anderson 1970), Stormberg Series of Fouriesburg, Orange Free State, South Africa.

Dromicosaurus gracilis: Partial skeleton (TM 123) from Red Beds of Naaupoort Nek, Bethlehem, Orange Free State, South Africa.

Thecodontosaurus dubius: Larger portion of a skeleton (SAM-3712) from the Cave Sandstone, Stormberg Series of Ladybrand, Orange Free State, South Africa.

Discussion

On the basis of the phalanges Seeley (1895*b*) stated that *Massospondylus carinatus* had a broad hind foot and Huene (1906) separated this genus from *Plateosaurus* mainly because of its *Thecodontosaurus*-like tibia. *Massospondylus* was the first genus of broad-footed prosauropod to be described from South Africa.

The manus (Fig. 7F–G, J) and the pes (Fig. 8L, N) of *Massospondylus harriesi* (SAM-3394) are obviously of the broad type. The material (Figs 7G, 8L, 12E) described by Van Hoepen (1920*b*) as *Massospondylus browni* should be referred to this species (Haughton 1924). The manus of *Aetonyx palustris* Broom (Fig. 7O) is of the broad type and the pes is similar, as indicated by the measurements given by Huene (1932: 92). J. Attridge (pers. comm.) regards *Aetonyx palustris* as a junior synonym for *Massospondylus harriesi*. The manus (Fig. 7Q) and pes (Fig. 8Q) of *Gryponyx africanus* are of the broad type and *Gryponyx africanus* is probably a junior synonym for *Massospondylus harriesi*.

Gryponyx taylori Haughton is a *nomen dubium* because the material is generically and specifically indeterminate; it probably represents another specimen of *Massospondylus harriesi*.

The manus and pes of *Dromicosaurus gracilis* Van Hoepen are not preserved but were probably of the broad type because *Dromicosaurus* was regarded as being closely allied to *Aetonyx* and *Massospondylus* by Van Hoepen (1920*b*), Haughton (1924) and Huene (1932). J. Attridge (pers. comm.) regards *Dromico-*

saurus gracilis as a junior synonym for *Massospondylus harriesi*. The type specimen of *Thecodontosaurus dubius* Haughton has never been figured, but Huene (1932: 92) referred it to *Aetonyx palustris* so it is presumably a broad-footed form; J. Attridge (pers. comm.) refers this specimen to *Massospondylus harriesi*.

Stratigraphically and geographically, *Massospondylus harriesi* is the most ubiquitous prosauropod in southern Africa.

Plateosaurus gracilis (Huene, 1907)

Thecodontosaurus (?) *hermannianus* Huene, 1907–08: 216, fig. 236, pl. 144 (fig. 1).
Plateosaurus gracilis Huene, 1932: 303.

Type

Right maxilla with teeth from the Stubensandstein (Upper Triassic) of Heslach, in Stuttgart, West Germany.

Lufengosaurus huenei Young, 1941*a*

Lufengosaurus hueni Young, 1941*a*: 1, figs 1–25, pls 1–6; 1947: 41; 1951: 50, fig. 11, pl. 12. Rozhdestvensky, 1965.
Gyposaurus sinensis Young, 1941*b*: 205, pls 1–9; 1948: 91, pls 1–5; 1951: 49.
Yunnanosaurus huangi Young, 1942: 64, figs 1–17; 1951: 56.
Lufengosaurus magnus Young, 1947: 2, figs 1–14.
Yunnanosaurus robustus Young, 1951: 58, figs 12–14, pls 7–10.

Types

Several incomplete skeletons from the lower Lufeng Series (Upper Triassic, Rhaetic) of Lufeng, Yunnan, China.

Discussion

Rozhdestvensky (1966) restudied 70 specimens from the Lufeng Series and decided that *Lufengosaurus huenei*, *L. magnus*, *Yunnanosaurus huangi*, *Y. robustus* and *Gyposaurus sinensis* of Young were all differentiated only on size-related characters and are conspecific (as *Lufengosaurus huenei* Young, 1941*a*). Rozhdestvensky (1966) noted that, judging from the original diagnosis of Young (1941*b*), *Gyposaurus sinensis* is hardly distinguishable from *G. capensis*, but that without visual comparisons or more detailed descriptions it is impossible to decide the relationship between these two species. Galton (1973, in press) noted that '*Gyposaurus*' *sinensis* was incorrectly referred to the genus *Gyposaurus*, and may represent a new genus or be based on juveniles of either *Lufengosaurus* or *Yunnanosaurus*. '*Gyposaurus*' *sinensis* should not be referred to the genus *Gyposaurus* (or *Anchisaurus*) because of the following anatomical features (Table 3):

1. Centra of posterior dorsal vertebrae are proportionally high with a central length to height ratio of 1,1 (Fig. 9O).
2. Anterior process of ilium is short and triangular (Fig. 10C).
3. Subacetabular part of pubis is broken but originally this region was

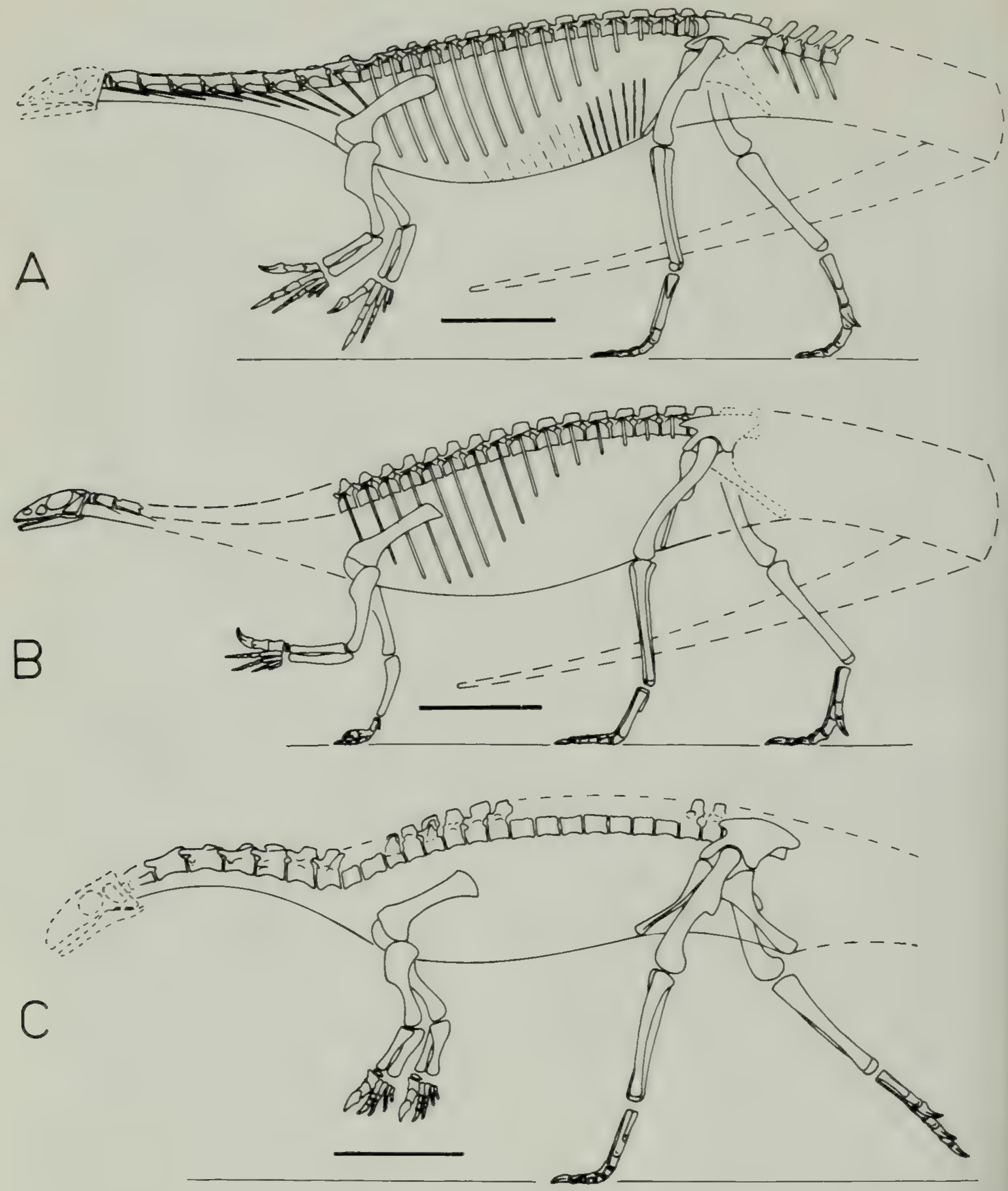

Fig. 12. Skeletal reconstructions of prosauropods. Scale = 20 cm. Tails of A and B diagrammatically folded over. A. *Efraasia diagnostica*, SMNS 12667, 12668, from Galton (1973). B. *Anchisaurus polyzelus*, YPM 1883, AM 41/109, from Galton (1973). C. *Lufengosaurus huenei*, based on figures of individual bones given by Young (1941*b*) as *Gyposaurus sinensis*.

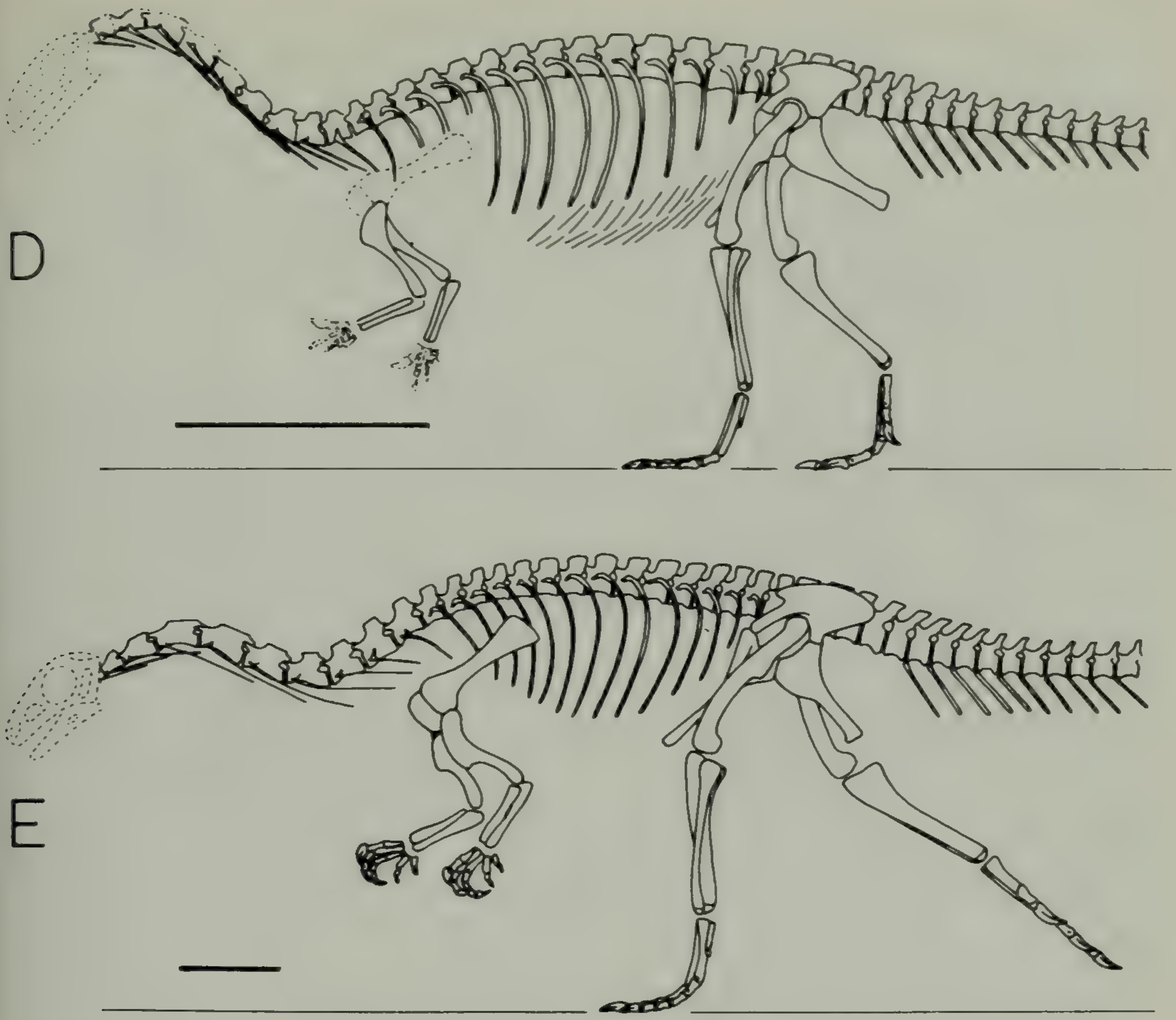

Fig. 12. (*cont.*)
D. *Aristosaurus erectus*, modified from *Gyposaurus capensis* of Huene (1932). E. *Massospondylus harriesi*, modified from *Thecodontosaurus browni* of Huene (1932), based on specimen described as *Massospondylus browni* by Van Hoepen (1920*a*).

deep with a complete obturator foramen (Young 1941*b*: 222; 1948: 96) (Figs 10I, L).

4. Pes (Fig. 8H) and manus (Fig. 7B) are broad.

Young (1941*b*) did not cite the papers of Broom (1906, 1911) so the assignment as *Gyposaurus sinensis* was probably based on the skeletal reconstruction of *Aristosaurus erectus* given by Huene (1932) as *Gyposaurus capensis*. However, the skeleton of '*Gyposaurus*' *sinensis* (Fig. 12C) differs greatly in several aspects from that of *Aristosaurus erectus* (Fig. 12D) and this is especially true for the form of the neck vertebrae (Fig. 9J) and fore limb. It should be noted that the skeletal reconstruction of '*Gyposaurus*' *sinensis* given by Young (1941*b*, pl. 9) bears practically no resemblance to a reconstruction (Fig. 12C) based on figures of the bones of the same specimen given by Young (1941*b*). The correctness of the contention of Rozhdestvensky (1966) that *Gyposaurus sinensis*

Young, 1941*b* is a junior synonym of *Lufengosaurus huenei* Young, 1941*a* is shown by the proportionally short neck and proportionally massive manus of the two types.

Prosauropoda *nomina dubia*

Gryponyx transvaalensis Broom, 1912

Gryponyx transvaalensis Broom, 1912: 82, figs 3–4. Van Hoepen, 1920*b*: 102. Haughton, 1924: 420. Huene, 1932: 91, pl. 7, fig. 5.

Type

Ungual 1 of the manus and a metatarsal (in the Transvaal Museum) from the Bushveld Sandstone (Cave Sandstone), Stormberg Series of Wiepe 1258, northern Transvaal, South Africa.

Discussion

This material is probably prosauropod but is generically and specifically indeterminate.

NON-PROSAUROPOD SPECIES INCORRECTLY ASSIGNED TO ANCHISAURIDAE

Order SAURISCHIA

Suborder THEROPODA

Arctosaurus osborni Adams, 1875

Arctosaurus osborni Adams, 1875: 177. Lydekker, 1889: 352.

Type

Isolated cervical vertebra (NMI 62 1971) from Heiberg Formation (Upper Triassic) of north-west extremity of Cameron Island, Bathurst Group, Arctic Archipelago, Canada.

Discussion

Arctosaurus was described as reptilian by Adams (1875) but subsequently Lydekker (1889) referred it to the family Anchisauridae. Regarded as a turtle by Huene (1906) and White (1973) but referred to the prosauropod family Melanorosauridae (as Plateosauravidae) by Huene (1956) and to the Anchisauridae (as Thecodontosauridae) by Romer (1966). The region of the diapophysis is slightly damaged (Fig. 13B, F) but from the adjacent curves of the neural arch (Fig. 13E) it is obvious that the diapophysis was very small and, as a result, this vertebra is from the anterior part of the series and is probably either the third or fourth cervical vertebra. It is proportionally very much shorter than the equivalent vertebrae of *Anchisaurus* (Figs 9H, 12B), *Efraasia* (Figs 9I, 12A) and *Plateosaurus* (Huene 1926). The only prosauropods with cervical vertebrae proportionally as short are *Thecodontosaurus* (Fig 11A) and *Lufengosaurus* (Figs 9J, 12C) but in both cases the vertebrae are proportionally much lower, the neural spines are not so well developed and there is no pleurocoel (exaggerated in *Arctosaurus* because of crushing). *Arctosaurus osborni* is

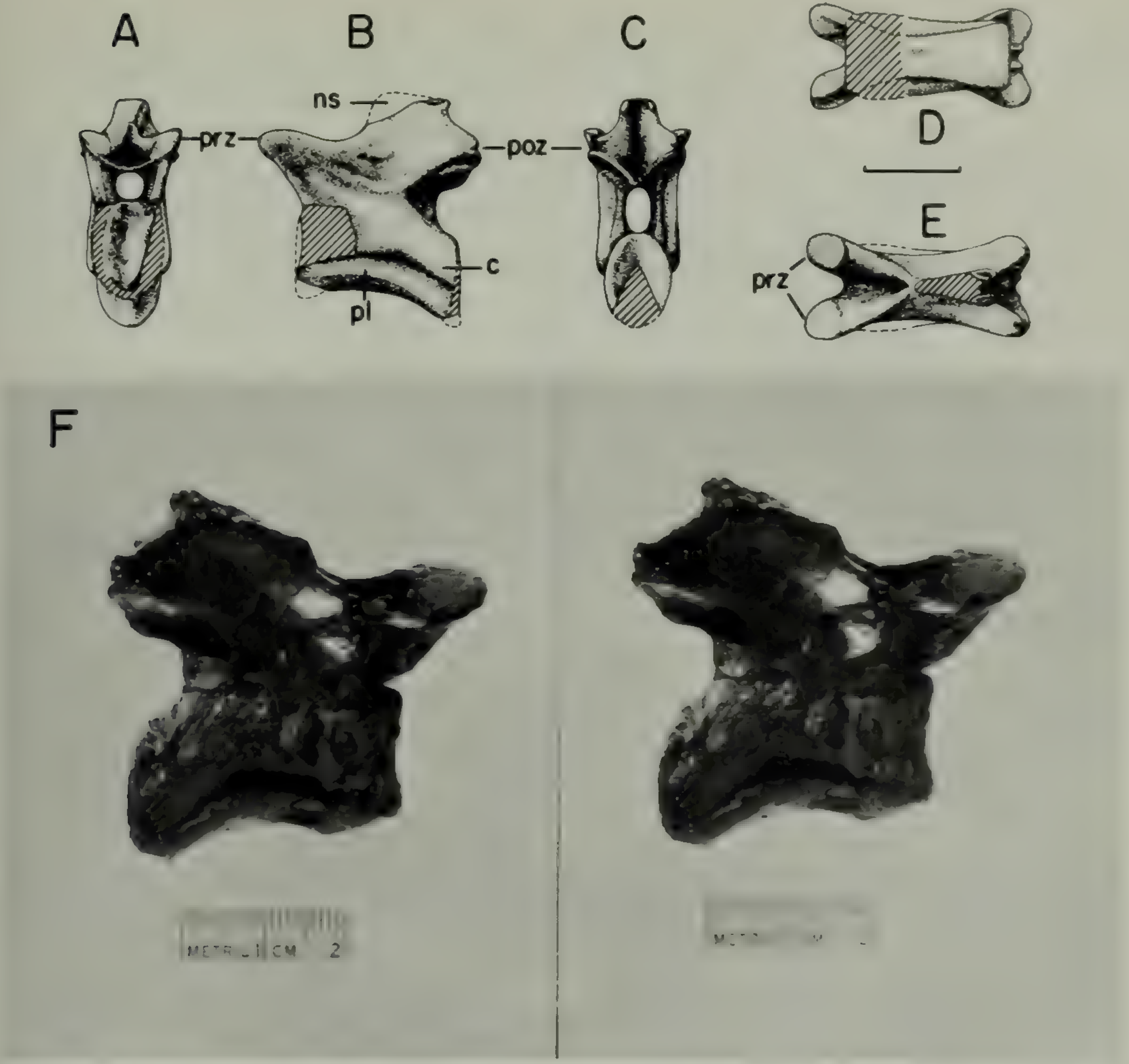

Fig. 13. *Arctosaurus osborni* Adams, holotype NMI G2 1971, anterior cervical vertebra in: A. Anterior view. B. Left lateral view. C. Posterior view. D. Ventral view. E. Dorsal view. F. Stereo photograph of left side, compare with B. Scale = 2,5 cm. Broken bone indicated by diagonal shading.

not a prosauropod and, on the basis of the general form of the vertebra and the presumed presence of a pleurocoel, this specimen is tentatively regarded as Theropoda *incertae sedis* as listed by Steel (1970).

Ischisaurus cattoi Reig, 1963

Ischisaurus cattoi Reig, 1963: 10, figs 4B, 5. Colbert, 1970: 27. Bonaparte, 1972*b*: 673, fig. 22.

Type

Two incomplete skeletons from the Ischigualasto Formation (lower Upper Triassic) of Argentina.

Discussion

Ischisaurus is listed as an anchisaurid by Steel (1970) and as Saurischia *incertae* by Bonaparte (1972*b*: 674), who notes that 'the suggested affinities with the Coelurosauria appears as one of the possible relationships'. Romer (1966) and Colbert (1970) list *Ischisaurus* as a coelurosaurian theropod.

Order THECODONTIA

'*Thecodontosaurus*' *gibbidens* Cope, 1878

Thecodontosaurus gibbidens Cope, 1878: 177. Huene, 1921: 571, figs 14–15.

Type

Isolated teeth from the Upper Triassic of Pennsylvania, U.S.A.

Discussion

The isolated teeth are almost circular rather than oval in cross-section as in prosauropods (*Thecodontosaurus antiquus* Riley & Stutchbury, 1840; *Anchisaurus*, YPM 1883; *Plateosaurus*. AMNH 6810), so these teeth are provisionally referred to the Ornithischia (Galton, in press).

Spondylosoma absconditum Huene, 1935

Spondylosoma absconditum Huene, 1935: 247, pl. 30, figs 1–13. Charig, 1967: 712. Colbert, 1970: 19. Bonaparte, 1972*b*: 674.

Type

Scapula, humerus, femur, tibia (all incomplete) and eight vertebrae from the Santa Maria Formation (Upper Triassic) of Brazil.

Discussion

Huene (1935, 1942) regarded *Spondylosoma* as a saurischian but did not make a more specific assignment for this genus. Romer (1956, 1966) referred *Spondylosoma* to the Anchisauridae (as Thecodontosauridae) as did Colbert (1970) and Charig (1967), who noted at the same time the possibility of its being a prestosuchid pseudosuchian. Bonaparte (1972*b*: 674) notes that 'there are doubts regarding its assignment to the Saurischia, or even to Prosauropoda. Unfortunately there are not sufficient diagnostic pieces to define better its taxonomic position' and *Spondylosoma* is listed as Saurischia *incertae*.

Teleocrater alphos (Haughton, 1932)

Thecodontosaurus (?) *alphos* Haughton, 1932: 662, fig. 19.
Teleocrater alphos Charig, 1967: 712.

Type

Two cervical vertebrae (SAM-10654) from the Manda Formation (Upper Triassic, Anisian) of Tanzania.

Discussion

Charig refers this material to the pseudosuchian *Teleocrater*.

Subclass LEPIDOSAURIA

Order LACERTILIA

Huene (1932, not 1931 as cited by Steel 1970) considered that the following Middle Triassic (Muschelkalk) species were based on specimens which should be referred to the eosuchian *Tanystropheus*, a lacertilian according to Wild (1974); the non-prosauropod nature of these species is also discussed by Colbert (1970):

Tanystropheus primus (Huene, 1907–08)

Thecodontosaurus primus Huene, 1907–08: pl. 42 (figs 8–9).
Tanystropheus primus Huene, 1932: 6.

Tanystropheus latespinatus (Huene, 1907–08)

Thecodontosaurus (?) *latespinatus* Huene, 1907–08: figs 237–245.
Tanystropheus latespinatus Huene, 1932: 6.

NOTES ON THE FAMILIES ANCHISAURIDAE AND PLATEOSAURIDAE

The infra-order Prosauropoda is currently divided into three families: Anchisauridae (= Thecodontosauridae), Plateosauridae and Melanorosauridae (see Romer 1956; Colbert 1964; Charig *et al.* 1965; Bonaparte 1972*a*). Postcranially the separation is clearest between melanorosaurids and non-melanorosaurids (Romer 1956: 617; Bonaparte 1972*a*: 160). Galton (1971, 1973) suggests that the range of morphological variation is insufficient to warrant the retention of two families of non-melanorosaurid prosauropods. However, the skulls of *Anchisaurus* (Fig. 9A) and *Plateosaurus* (Fig. 9C) are very different and, because of this, Galton (in press) now considers that they should not be included in the same family. Fortunately the genera concerned are the basis for the first two valid prosauropod family names to be proposed: Anchisauridae Marsh, 1885, and Plateosauridae Marsh, 1895.

In only one case (*Anchisaurus polyzelus*, YPM 1883) is a well-preserved skull found in natural association with a skeleton of a slender-footed prosauropod. Consequently the referral of *Efraasia* and *Thecodontosaurus* to the Family Anchisauridae is tentative. Contrary to the impression given by Huene (1932: fig. 7; 1956: fig. 10), the skull of *Efraasia* is very incomplete but, as noted by Galton (1973), *Efraasia* is an ideal ancestor for the more recent *Anchisaurus*. The holotype of *Thecodontosaurus antiquus* is an incomplete dentary but, judging from what is preserved (Fig. 9B), the complete lower jaw was probably more like that of *Anchisaurus* (Fig. 9A) than that of *Plateosaurus* (Fig. 9C). Although considered unlikely, the discovery of additional material may show that the restriction of the family Anchisauridae to slender-footed forms is artificial. However, the criterion is practical and with it most taxa and specimens of non-melanorosaurid prosauropods are readily referable to either the Family Anchisauridae or the Family Plateosauridae.

Plateosaurus engelhardti Meyer, 1837 from the Keuper (Upper Triassic) of Germany is the earliest taxon of plateosaurid to be described, but since then a multitude of taxa have been erected for material from the Triassic of Germany (Steel (1970) lists 9 species as *Plateosaurus*, 8 species as *Gresslyosaurus*). However, this material is probably extremely overclassified and all the taxa of European plateosaurids listed by Steel (1970: 53–56) should be provisionally regarded as junior synonyms of *Plateosaurus engelhardti* Meyer, 1837. All the European plateosaurid material can probably be referred to (at the most) three species of *Plateosaurus*, but a restudy of all the holotypes is needed to determine the other valid species.

Lufengosaurus (see Young 1941*a*, *b*, 1942, 1947, 1951) and *Plateosaurus* (see Huene 1907–8, 1926, 1932) possess the features listed above as characteristic of plateosaurids. The skulls of *Ammosaurus* (see Galton, in press) and *Aristosaurus* (see Van Hoepen 1920*a*) are not well enough preserved to tell anything about the form of the skull. However, the holotype of *Massospondylus harriesi* includes a lower jaw (Fig. 9D), the posterior part of which is deep with the articulation offset ventral to the line of the tooth row. J. Attridge is studying two skulls of *Massospondylus harriesi* (SAM- K388 and K1314) and has found that both skulls show the features listed above (pers. comm.).

Massospondylus is the most ubiquitous prosauropod in southern Africa and its previous classification as an anchisaurid made the prosauropod fauna of Africa unique, because in other areas with abundant, well-preserved prosauropod skeletons, plateosaurids are the most common form. However, Cox (1973: 213) notes that 'it is clear that land connections between all the continents existed for much, at least, of the Triassic'. As regards prosauropods the presence of *Anchisaurus* in North America and South Africa and the presence of *Plateosaurus* in Germany and South America (Casamiquela 1964; Bonaparte 1972*b*) indicated that this was the case for the continents on either side of the Atlantic. With the transfer of broad-footed forms, previously listed under the Anchisauridae, to the Plateosauridae, this family becomes the dominant and cosmopolitan prosauropod family of the world. In marked contrast, the Anchisauridae have an extremely restricted fossil record (total of about 10 articulated specimens for North America, Europe and South Africa) with no remains discovered to date from Asia (Young 1951; Rozhdestvensky 1966) or South America (Bonaparte, pers. comm.). Haughton (1924) noted that the Stormberg Series of South Africa was deposited under conditions of progressively increasing aridity, and it is interesting that skeletal remains of melanorosaurids occur in the lowermost levels (Passage Beds, Charig *et al.* 1965; basal Red Beds, Haughton 1924), most plateosaurid skeletons occur higher in the Red Beds, and those of anchisaurids are found in the overlying Cave Sandstone (Charig *et al.* 1965; Haughton 1924; Haughton & Brink 1956). Charig *et al.* (1965) report the presence of small tridactyl footprints in the Passage Beds and in the lower Red Beds and note (p. 204) that these '. . . may indicate the movement of thecodontosaurids from one upland region to another via a lowland area'. The world-wide rarity of anchisaurid skeletal remains is presumably because these species occupied the drier upland areas, which are rarely represented in the fossil record.

SUMMARY

The holotype (SAM-990) of the prosauropod dinosaur *Anchisaurus capensis* (Broom, 1911) is characterized by the following combination of characters: low centra to posterior dorsal vertebrae, broad bases to neural spines of anterior caudal vertebrae, ilium with long anterior process, pubis with open obturator foramen, and with slender pes with first ungual phalanx the largest. SAM-990 differs from the North American *Anchisaurus polyzelus* (Hitchcock) only in the large size of the first ungual of the pes, and SAM-990 is referred to *Anchisaurus* Marsh, 1885 as *Anchisaurus capensis* (Broom). Taxa which have been incorrectly referred to the genus *Gyposaurus* (= *Anchisaurus*) are *Gyposaurus erectus* (Van Hoepen) (= *Aristosaurus erectus* Van Hoepen), *Gyposaurus sinensis* Young (= *Lufengosaurus huenei* Young) and *Gyposaurus skirtopodus* (Seeley) (= *Hortalotarsus skirtopodus* Seeley, *nomen dubium*). The Family Anchisauridae is restricted to those species with slender feet, *viz. Anchisaurus polyzelus*, *A. capensis*, *Efraasia diagnostica*, and *Thecodontosaurus antiquus*. Taxa with broad feet previously classified as anchisaurids (*Aristosaurus*, *Ammosaurus*, *Gyposaurus sinensis* (as *Lufengosaurus huenei*), *Massospondylus* (including *Aetonyx*, *Dromicosaurus*, *Gryponyx africanus*, *G. taylori*, *Thecodontosaurus dubius*), *Yunnanosaurus* (= *Lufengosaurus*) are transferred to the family Plateosauridae, the dominant and cosmopolitan family of prosauropods.

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ABBREVIATIONS

acetabulum	acet
anterior process of ilium	ant proc
astragalus	as
centrum	c
caudal vertebra	ca
calcaneum	cal
chevron	ch
dorsal vertebra	dor
neural spine	ns
pleurocoel	pl
postzygapophysis	poz
prezygapophysis	prz

pubic peduncle	pub ped
sacral vertebra	sac
Amherst College Museum, Amherst, Massachusetts	AM
American Museum of Natural History, New York	AMNH
British Museum (Natural History), London	BMNH
National Museum of Ireland, Dublin	NMI
South African Museum, Cape Town	SAM
Staatlichen Museum für Naturkunde in Stuttgart	SMNS
Yale Peabody Museum, New Haven, Connecticut	YPM

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Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. n., sp. n., comb. n., syn. n., etc.

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Family Nuculanidae

Nuculana (*Lembulus*) *bicuspidata* (Gould, 1845)

Figs 14–15A

Nucula (*Leda*) *bicuspidata* Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (figs 8a–b).
Nucula largillierti Philippi, 1861: 87
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9

Note punctuation in the above example:
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In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33.51S, 25.39E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and of date.

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'. . . in *C. namacolus* (Fig. 10) . . .'

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Von Huene but F. von Huene

(c) Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

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Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

P. M. GALTON & M. A. CLUVER

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By

H. C. KLINGER, W. J. KENNEDY & W. G. SIESSER

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YABEICERAS (CONIACIAN AMMONITE) FROM THE ALPHARD GROUP OFF THE SOUTHERN CAPE COAST

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(With 4 figures)

[*MS accepted 30 October 1975*]

ABSTRACT

During dredging operations off the southern Cape coast a bored concretion containing a specimen of the ammonite *Yabeiceras manasoaense* Collignon was recovered. The species had been previously recorded only from the Coniacian of Madagascar and Japan; the occurrence extends the geographic range of the species and provides reliable dating for the outcropping offshore Mesozoic Alphard Group of sediments of the area.

CONTENTS

	PAGE
Introduction	161
Material	161
Systematic Palaeontology	162
Acknowledgements	167
References	167

INTRODUCTION

During dredging operations off the southern Cape coast, undertaken by the Marine Geoscience Unit of the University of Cape Town, a concretion containing an ammonite was brought to the surface at 35.06S, 20.32E from a depth of 110 metres. The specimen was identified as belonging to the genus *Yabeiceras*, thus far only described from the Coniacian stage of the Upper Cretaceous of Madagascar and Japan. Apart from adding to our knowledge of the geographical distribution of the genus, this record permits a precise dating of the offshore Alphard Group of sediments in the area. The only other recorded Mesozoic ammonite from the South African offshore is an *Eubaculites* sp. recorded by Dingle (1973: 10), although occurrences of Tertiary nautiloids were reported by Cayeux (1934) and Miller & Furnish (1956).

MATERIAL

The concretion containing the ammonite consists of a dark greyish-green, fine-grained quartz siltstone, with a calcite cement. The ammonite itself is

Ann. S. Afr. Mus. **69** (7), 1976: 161–168, 4 figs.

partially filled with sparry calcite, but the greater part is preserved as an internal mould, consisting of the same material as the concretion. Part of the original aragonitic shell has been preserved.

That part of the concretion and the ammonite which was exposed at the sediment/water interface is pitted with two types of borings of Recent organisms. The first consists of large (up to 1 cm in diameter) flask-like crypts, internally smooth, with a constricted aperture. The second is much smaller, 2 to 3 mm across and irregular in habit. Both types of borings show cross-cutting relationships. The larger may be ascribed to lithodomous bivalves, the smaller to polychaete worms, and perhaps other organisms. Apart from a few encrusting ectoprocts (bryozoans) and serpulids, most of which occur within the borings, no other epizoans are present.

SYSTEMATIC PALAEONTOLOGY

Family **Collignoniceratidae** Wright & Wright, 1951

Subfamily Barroisiceratinae Basse, 1947

Genus *Yabeiceras* Tokunaga & Shimizu, 1926
(= *Eboroceras* Basse, 1947)

Type species

Yabeiceras orientale Tokunaga & Shimizu, 1926 by original designation.

Discussion

Matsumoto *et al.* (1964; Matsumoto 1969) have provided recent reviews of *Yabeiceras* and demonstrated that it should be referred to the Barroisiceratinae rather than to the Peroniceratinae, as in the current *Treatise* (Wright 1957: L429).

Yabeiceras is an uncommon genus represented by four species in Japan: *Y. orientale* Tokunaga & Shimizu, *Y. kotoi* Tokunaga & Shimizu, *Y. himuroi* Tokunaga & Shimizu, and *Y. manasoaense* Collignon, whilst Basse (1946) and Collignon (1965) record six species from Madagascar: *Y. magnumtuberculatum* Basse, *Y. manasoaense* Collignon, *Y. menabense* Collignon, *Y. costatum* Collignon and *Y. ankinatsyense* Collignon. Undescribed species also occur in Zululand (Kennedy & Klinger 1975). All records of *Yabeiceras* are of either Lower or Middle Coniacian age.

Yabeiceras manasoaense Collignon, 1965
Figs 1–4

Yabeiceras manasoaense Collignon, 1965: 84, pl. 452 (fig. 1839).
Matsumoto 1971: 144, pl. 24 (55) (fig. 2), text-fig. 9 (110).

Holotype

The specimen figures by Collignon (1965, pl. 452 (fig. 1839)) from the Coniacian of Manasoa (Betioky), Madagascar.

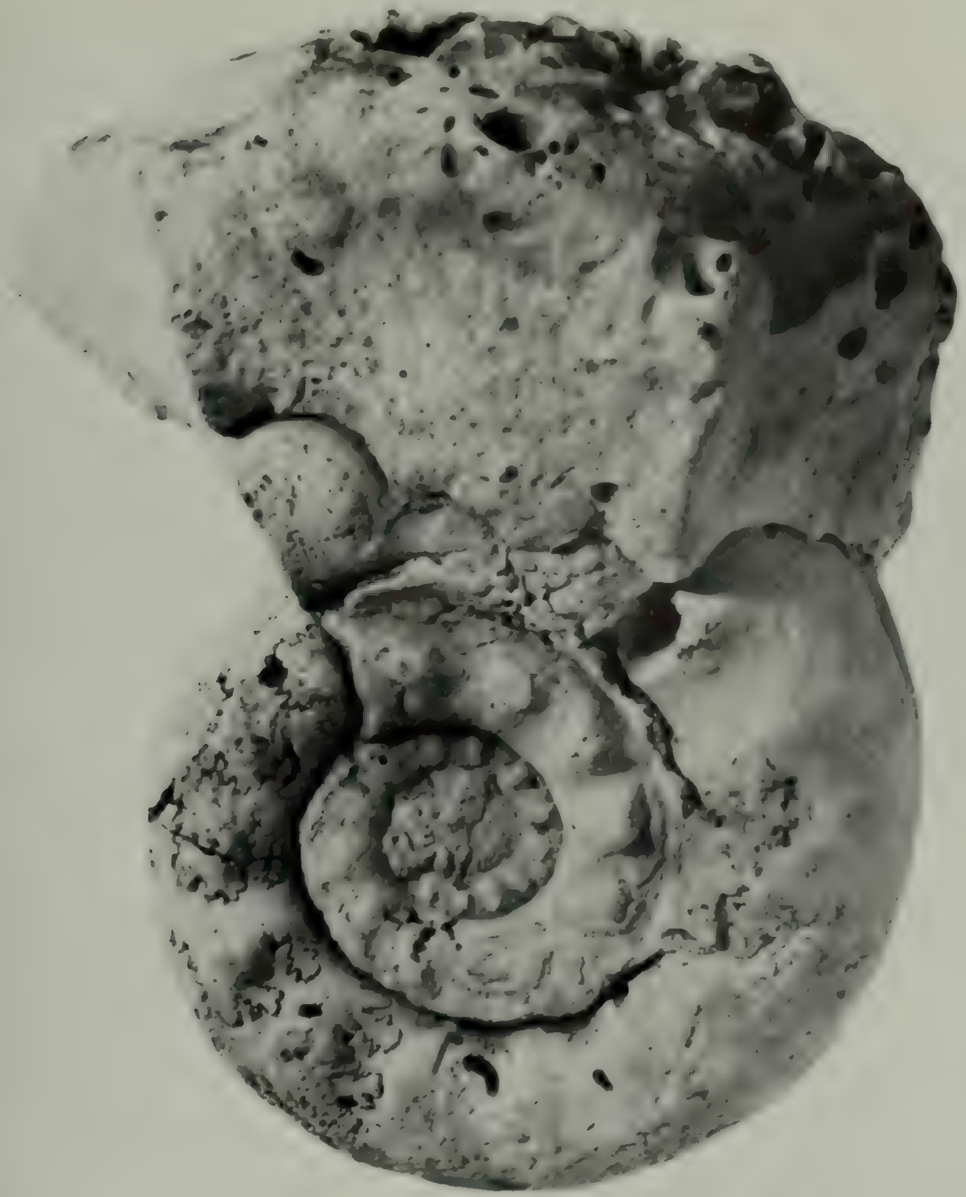

Fig. 1. *Yabeiceras manasoaense* specimen 4492 left lateral view × 1.

Material

Sample 4492 from the Alphard Group at 35.06S, 20.32E, and housed with the Marine Geoscience Unit, University of Cape Town collections.

Description

The specimen comprises just over two whorls of phragmocone and an incomplete body chamber of slightly more than a third of a whorl. The innermost whorls up to a diameter of 10 mm are not preserved. Coiling is very evolute with an umbilical diameter of 54,6 per cent of the total diameter. The outer whorls embrace only slightly, covering less than 10 per cent of the previous

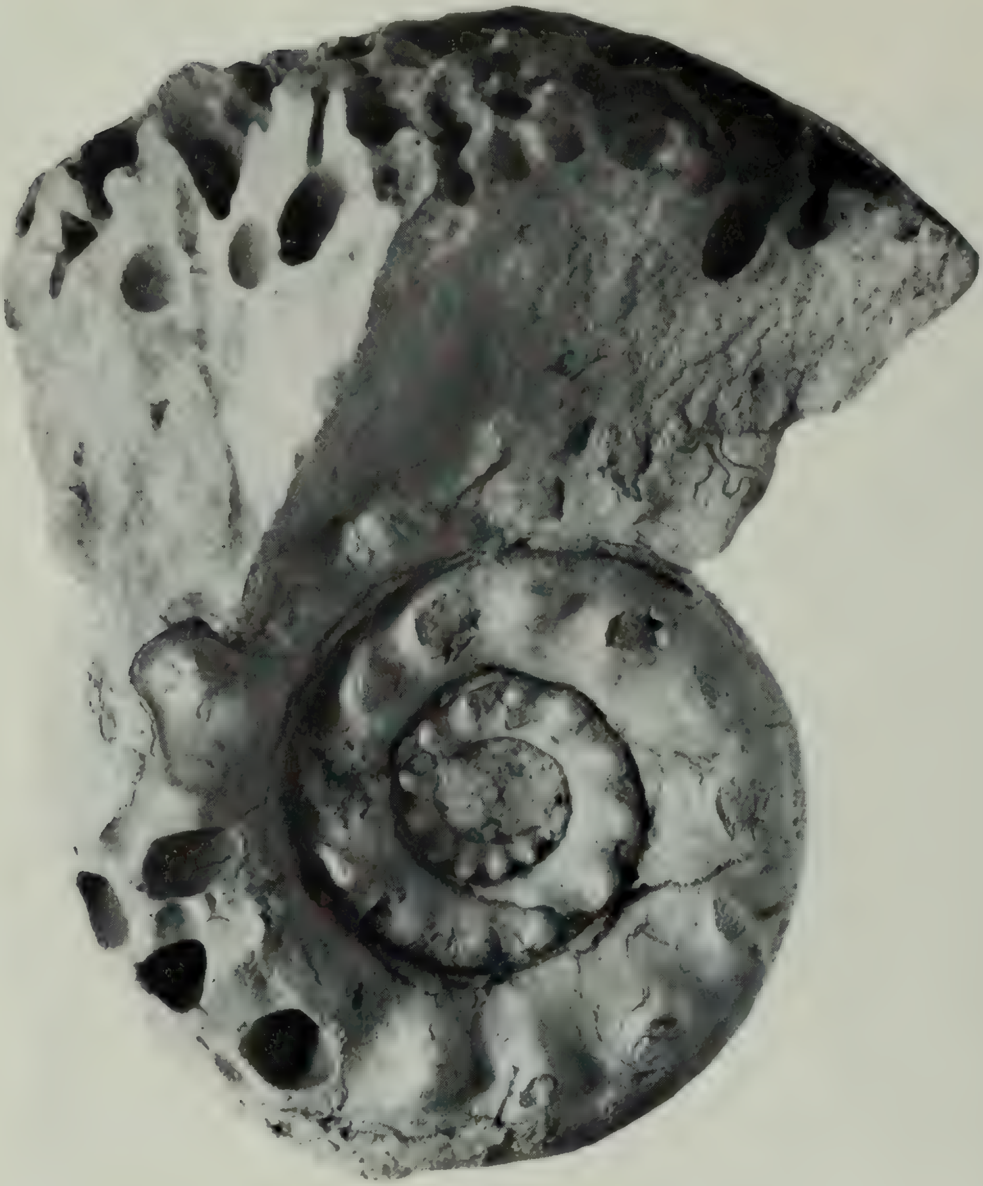

Fig. 2. *Yabeiceras manasoaense* specimen 4492 right lateral view × 1.

whorl. The whorl section of the body chamber is coronate, with maximum breadth across the dorsal third of the flanks. The venter is ornamented by a low broad keel, bounded on either side by two equally broad depressions, in turn flanked by low lateral keels.

Flank ornament consists of a single row of tubercles numbering sixteen on the outer whorl. On the inner whorls the tubercles are conical to pointed, and are housed in notches in the umbilical wall of the succeeding whorl. With increasing diameter the tubercles become more bullate and migrate progressively from the umbilical suture towards the midflank, and eventually to the dorsal third of the flanks. Ornament declines markedly on the body chamber.

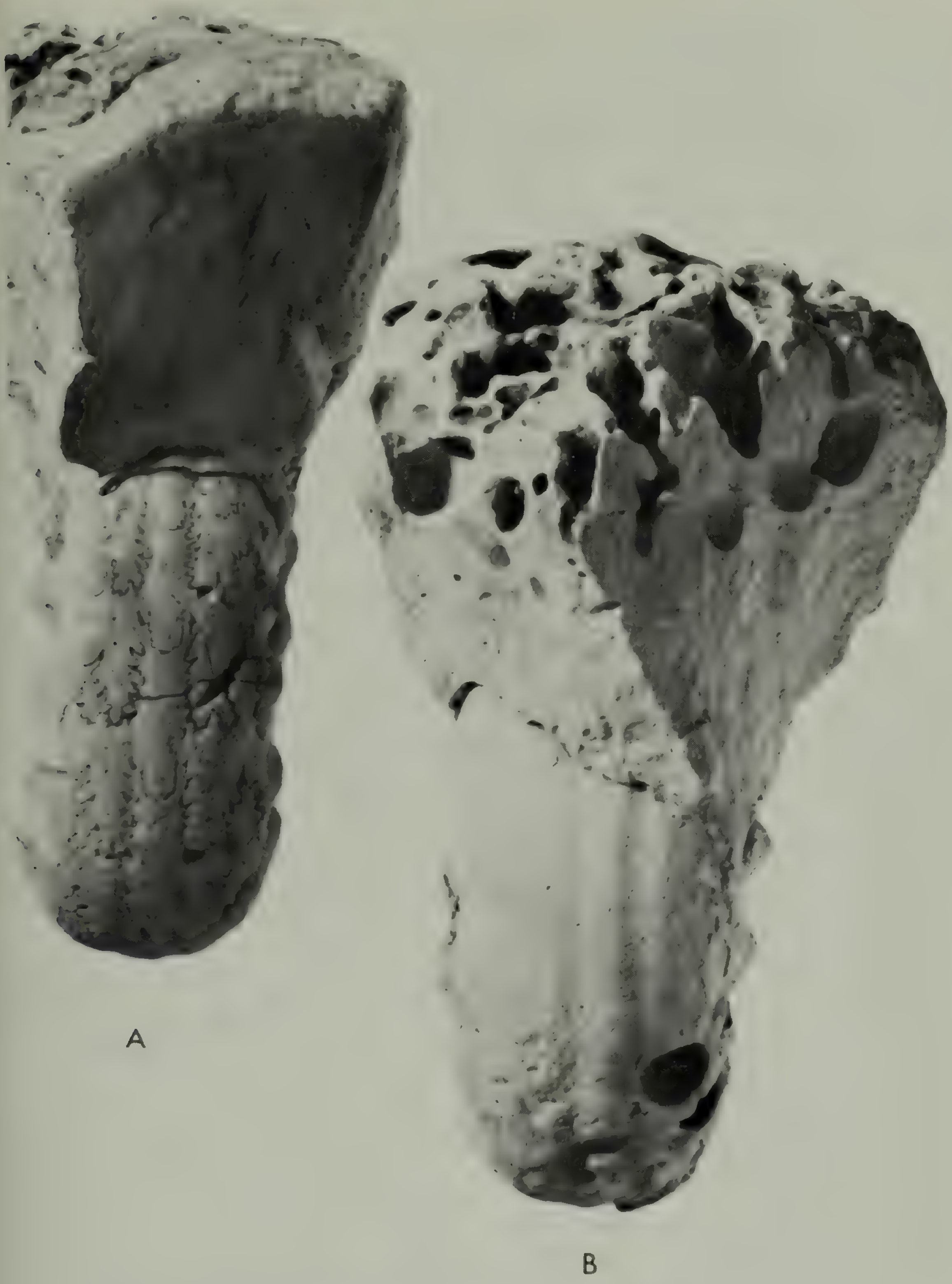

Fig. 3. *Yabeiceras manasoaense* specimen 4492. A. Ventral view × 1. B. Dorsal view × 1.

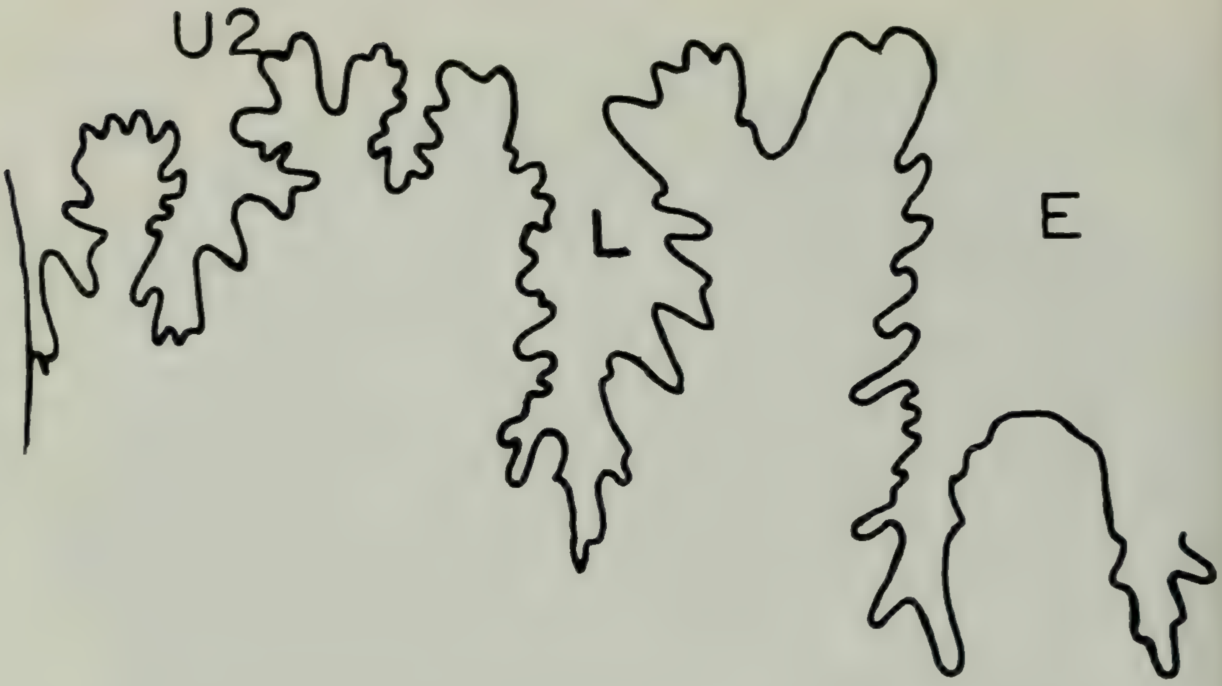

Fig. 4. External suture line of *Yabeiceras manasoaense* Collignon, specimen 4492 at whorl breadth of 30 mm × 3.

Dimensions

Specimen	D	Wb	Wh	Wb/Wh	U
4492	92,5	34(36,9)	21,5(23,2)	1,5	50,5(54,6)
Holotype . . . . (Collignon 1965)	105	37(35)	24(23)	1,5	51(49)
Matsumoto 1971 . . (Muramoto coll. Ob-S-6-p1)	149	38,6(26)	43,2(29)	0,9	72,4(48)

Discussion

Differences between the nine described species of *Yabeiceras* are slight, and well within the range of variation documented in related ammonite groups. Study of large populations will probably show that most of the described forms are variants of one or two variable species. Available material is inadequate for any constructive discussion of this point, however. The present specimen compares most closely with *Yabeiceras manasoaense*, showing a similar whorl section and ornament which declines on the outer whorls. Dimensions are closely similar to that of the holotype. The larger specimen figured and described by Matsumoto (1971: 144, pl. 24 (fig. 2)) is virtually identical at similar diameters, and shows further development of the declining ornament seen on the body chamber of our specimen.

Yabeiceras bituberculatum Collignon (1965: 821, pl. 451 (fig. 1836), pl. 452 (fig. 1838)) is readily distinguished on the basis of the presence of ventral tubercles when young, whilst Collignon's figure shows what appears to be a siphonal row of elongate clavi rather than a continuous keel at this diameter, whilst the adult body chamber is remarkably smooth and constricted.

Yabeiceras magnumbilicatum (Basse) (1946: 73, fig. 2, pl. 2 (figs 2a–b); Collignon 1965: 82, pl. 451 (fig. 1836)) has larger, coarser umbilical nodes, a contracted, virtually smooth body chamber, and far more involute coiling (U = 35 per cent of diameter).

Y. costatum Collignon (1965: 87, pl. 454 (fig. 1841)) is a costate, rather than tuberculate species, with 26–28 ribs per whorl, as is *Y. ankinatsyense* Collignon (1965: 87, pl. 454 (fig. 1842)).

Y. menabense Collignon (1965: 86, pl. 453 (fig. 1840)) is characterized by a very depressed whorl section, evolute coiling and 12–15 massive tubercles per whorl.

Y. magnumbilicatum, *Y. bituberculatum* and *Y. manasoaense* are contemporaries, as are *Y. menabense*, *Y. costatum* and *Y. ankinatsyense*. It is difficult to see these as more than one, or perhaps two species, whilst the *Y. costatum* group is scarcely distinguishable from the type species, *Y. orientale* or the costate *Y. himuroi* and *Y. kotoi* (Tokunaga & Shimizu 1926).

Occurrence:

Y. mansoaense is recorded from the Lower to Middle Coniacian of Japan and the Middle Coniacian *Kossmaticeras theobaldianum*/*Barroisiceras onilahyense* Zone of Madagascar. In Zululand related, but as yet undescribed, forms occur in the St. Lucia Formation in the second division of the Coniacian, associated with *Forresteria alluaudi* (Boule, Lemoine & Thevenin), *Proplacenticeras* spp. and other forms, again suggesting an early Coniacian age.

ACKNOWLEDGEMENTS

We should like to express our thanks to the Marine Geoscience Unit for placing the material and data at our disposal. Thanks are due to Mr Neville Eden for the photography.

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Nuculana (*Lembulus*) *bicuspidata* (Gould, 1845)

Figs 14–15A

Nucula (*Leda*) *bicuspidata* Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (figs 8a–b).
Nucula largillierti Philippi, 1861: 87
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

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THE CRANIAL AND CERVICAL MUSCLES OF THE SOUTH AFRICAN LIMBLESS LIZARD *TYPHLOSAURUS AURANTIACUS AURANTIACUS* PETERS (REPTILIA, SAURIA)

By

JURI A. VAN DEN HEEVER

Cape Town Kaapstad

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By

Juri A. van den Heever

South African Museum, Cape Town

(With 18 figures)

[*MS accepted 25 November 1975*]

ABSTRACT

The skull and cervical vertebrae of *Typhlosaurus aurantiacus aurantiacus* exhibit marked adaptations to a fossorial mode of life which is reflected in the associated musculature. Neither eye muscles nor supratemporal arches are present. The adductor musculature of the jaws, compacted into the temporal region, are dominated by two tripartite tendons, the bodenaponeurosis and the quadrate tendon. The m. pseudotemporalis is single. The m. cervicomandibularis is probably the major jaw opening muscle. Posttemporal fenestrae are absent and the cervical musculature encroaches far anteriorly on to the bulbous occiput. Discussed in terms of a lever of the third class the action of the jaw shows great similarity to that of a non-fossorial skink like *Mabuia*, and probably functions in an identical manner. Primary adaptations for a fossorial mode of life appear to be the strengthening and streamlining of the skull, loss of limbs and limb girdles and general attenuation of the body.

CONTENTS

Introduction 169
Material and methods 171
Description
Osteology
Cranial osteology 171
Cervical osteology 179
Myology
Muscle classification and nomenclature . 181
Constrictor dorsalis group 182
Adductor mandibulae group 184
Intermandibular musculature 194
Tongue musculature 195
Depressor mandibulae group 197
Cervical musculature 202
Discussion and conclusions 204
Acknowledgements 210
References 210
Abbreviations 213

INTRODUCTION

The doubtful taxonomic position of *Typhlosaurus* has been dealt with by various authors. Boulenger (1887) regarded the genus as related to *Acontias* but placed it, like Gadow (1901), together with *Anelytropsis* and *Feylinia* in the family Anelytropidae, close to the Scincidae. Camp (1923) places *Typhlosaurus*

Ann. S. Afr. Mus. **69** (8), 1976: 169–214, 18 figs

in the Feyliniidae, within the superfamily Scincoidea, together with the Scincidae, the Anelytropsidae and the Dibamidae.

Hewitt (1929), De Witte & Laurent (1943) and FitzSimons (1943) also refer the genus to the Scincidae and according to Smit (in press) FitzSimons regards *Typhlosaurus* as derivable, via Aconthophiops, from *Acontias*. Romer (1956) rather doubtfully includes *Typhlosaurus* within the Scincidae. Greer (1970), on the basis of the external morphology and cranial osteology especially the relationship of the frontal bones and the bones of the secondary palate, regards *Acontias*, *Aconthophiops* and *Typhlosaurus* as a subfamily of the Scincidae, i.e. the Acontinae. Broadley (1968) agrees with FitzSimons and states: 'The genus *Typhlosaurus* appears to have been derived from an ancestral form of *Acontias*, after passing through an intermediate stage which is demonstrated by the monotypic genus *Aconthophiops*.' According to Smit (1964) the close relationship between *Typhlosaurus* and *Acontias* is abundantly confirmed by the cranial osteology of *T. caecus*, indicating that the genus *Typhlosaurus* undoubtedly belongs within the Scincidae.

The following classification is thus adopted.

Class: Reptilia
Order: Squamata
Suborder: Sauria
Family: Scincidae
Subfamily: Acontinae Greer, 1968
Genus: *Typhlosaurus* Wiegmann, 1834
Species: *T. aurantiacus* Peters, 1882
Subspecies: *T. aurantiacus aurantiacus* Broadley, 1968.

Limbless skinks of the genus *Typhlosaurus* are confined to southern Africa (Broadley 1968). Eight species were recorded by FitzSimons (1943), and one additional species, the greatly attenuated *T. braini* from the Namib Desert, was described by Haacke (1964). Subsequently Broadley (1968) revised the genus, recognizing eight species placed into three species groups.

The genus as a whole is fossorial and according to Mertens (1955) only appears on the surface towards evening. Their diet includes small insects and myriapods of which small beetle larvae and termites form the most important groups (Broadley 1968).

The cranial osteology of the fossorial Scincidae and forms with scincid affinities, such as *Dibamus*, are well known from the work done on *Acontias* (De Villiers 1939; Brock 1941; Van der Merwe 1944), *Dibamus* (Gasc 1968; De Weerdt 1971), *Typhlosaurus* (Smit 1964), *Feylinia* (Du Toit 1971), *Typhlacontias* (Cluver 1965), *Melanoseps* (Boyd 1969) and *Scelotes* (Leonard 1973).

The postcranial skeleton is less well known and except for the work of Gasc (1967*a*, *b*, *c*; 1968) and Hofstetter & Gasc (1969) has attracted few investigators.

Myological studies on limbless lizards are few and far between. According to Auffenberg (1962) there is no record of the axial muscles of limbless lizards up to that time. Except for the work of Gasc (1968), De Weerdt (1971) and Leonard (1973) the cranial muscles of limbless lizards are largely unknown. De Weerdt's account differs from the more detailed description of Gasc. However, Gasc's description is difficult to evaluate in the light of comments given by Haas (1973), and Leonard discusses only the eye muscles in *Scelotes.*

Haas (1973) reviews the jaw muscles of the Rhynchocephalia and the Squamata stating that: '. . . detailed studies of the cranial muscles are lacking for two families (or groups often considered to be families) of lizards, namely the Anelytropsidae and the Feyliniidae'. Greer (1970) assigned these two groups to the Scincidae as the subfamilies Acontinae and Feylininae. Together they represent the fossorial Scincidae of which the above statement is certainly true.

The previously mentioned studies have shown that a fossorial habit produces distinctive skeletal changes. Change in skeletal proportions should inevitably affect associated musculature and in view of this fact the acute lack of literature on the myology of fossorial Scincidae is believed to sufficiently justify this paper.

MATERIAL AND METHODS

Three alcohol-fixed specimens of *Typhlosaurus aurantiacus* were obtained from the South African Museum. One specimen was dissected and the skull and postcranial skeleton were used for comparative and photographic purposes. Both the other specimens were decalcified for a period of seven days in 7,5 per cent solution of nitric acid in 70 per cent alcohol. Subsequently the specimens were separately dehydrated, cleared in terpineol and embedded in paraffin wax (52–54°C). Sectioned at 20 microns, one specimen gave excellent results; the other proved of no use and was discarded. Staining and counter-staining were done with the azocarmine-azan method and the enlarged drawings of the sections were made with the aid of a camera lucida microscope attachment.

Owing to the paucity of material several specimens of the related but more abundant genus *Acontias* were dissected to elucidate gross topography.

DESCRIPTION

OSTEOLOGY

Cranial osteology

The skull of *Typhlosaurus caecus*, which closely resembles that of *T. aurantiacus*, was described by Smit (1964), and the reader is referred to this paper for a comprehensive account of the cranial osteology. However, prior to embarking on a description of the myology, the cranial and the cervical osteology merit a few additional remarks on certain areas important to muscle attachments, where Smit's description is inadequate for the purpose of this paper

T. aurantiacus has the elongate skull and reduced orbits common to attenuate fossorial lizards (Figs 1A–B, 2A). The eyes are visible as inconspicuous black dots through the transparent integument and are devoid of associated musculature. However, an optic nerve is present and the retinal pattern resembles

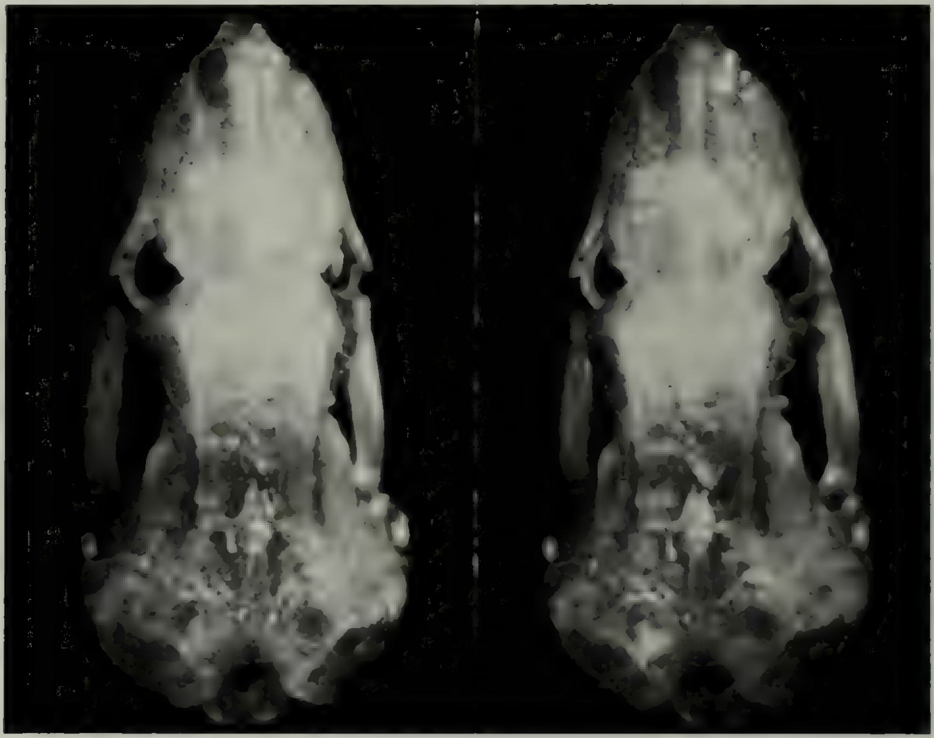

Fig. 1A. Stereophotographs of *Typhlosaurus aurantiacus* skull; dorsal view.

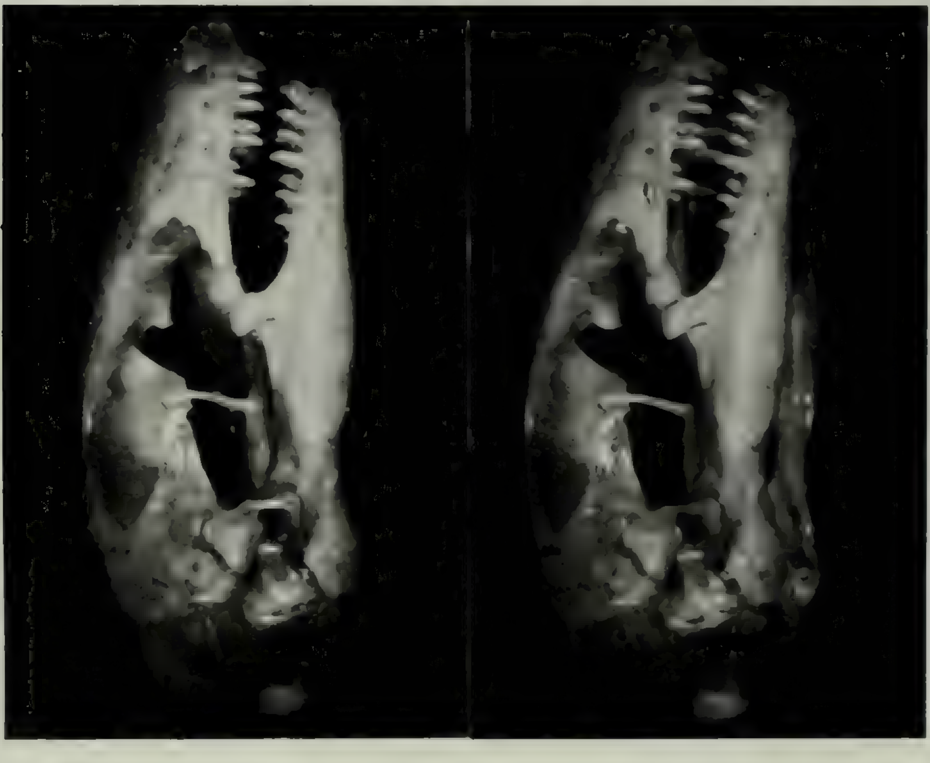

Fig. 1B. Stereophotographs of *Typhlosaurus aurantiacus* skull; lateral view.

that of amphisbaenids, in which light perception has been demonstrated by Bonin (1965).

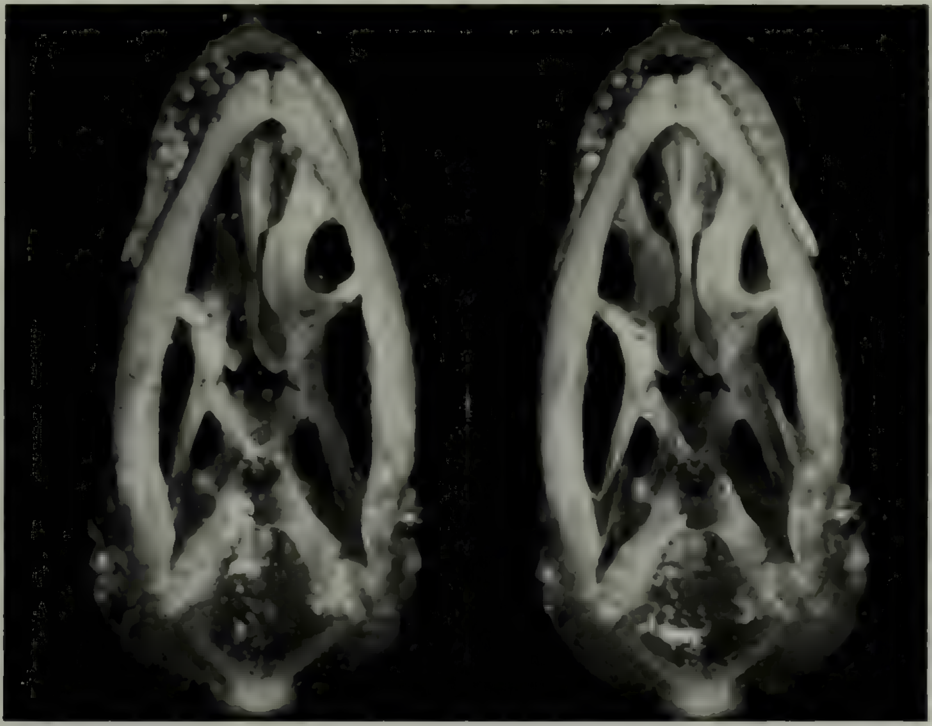

Fig. 2A. Stereophotographs of *Typhlosaurus aurantiacus* skull; ventral view.

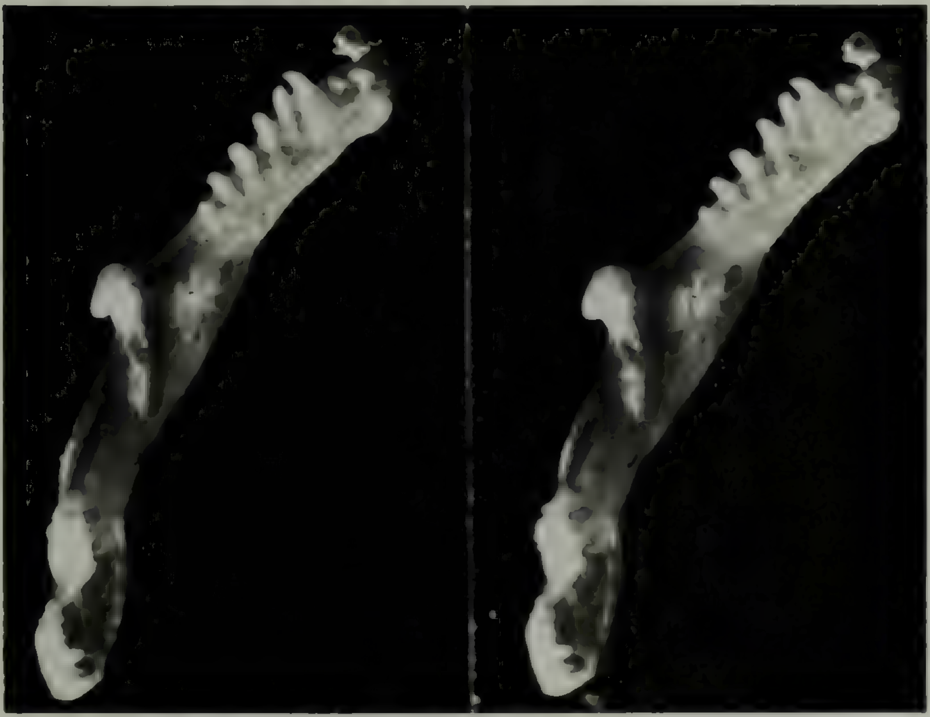

Fig. 2B. Stereophotographs of *Typhlosaurus aurantiacus* lower jaw; lingual view.

No remnants of lacrimal bones were found. The supratemporal arch is absent but both the squamosal and supratemporal bones are present as small, flattened, slightly overlapping elements dorsal to the quadrate.

The squamosal, lying anterolateral to the supratemporal, is tendinously connected to the quadrate head (Figs 3, 13). The supratemporal lies posteromedial to the squamosal and shares with the much reduced paroccipital process of the otic capsule the articulation with the quadrate head by means of a pad of fibrocartilage (Fig. 3).

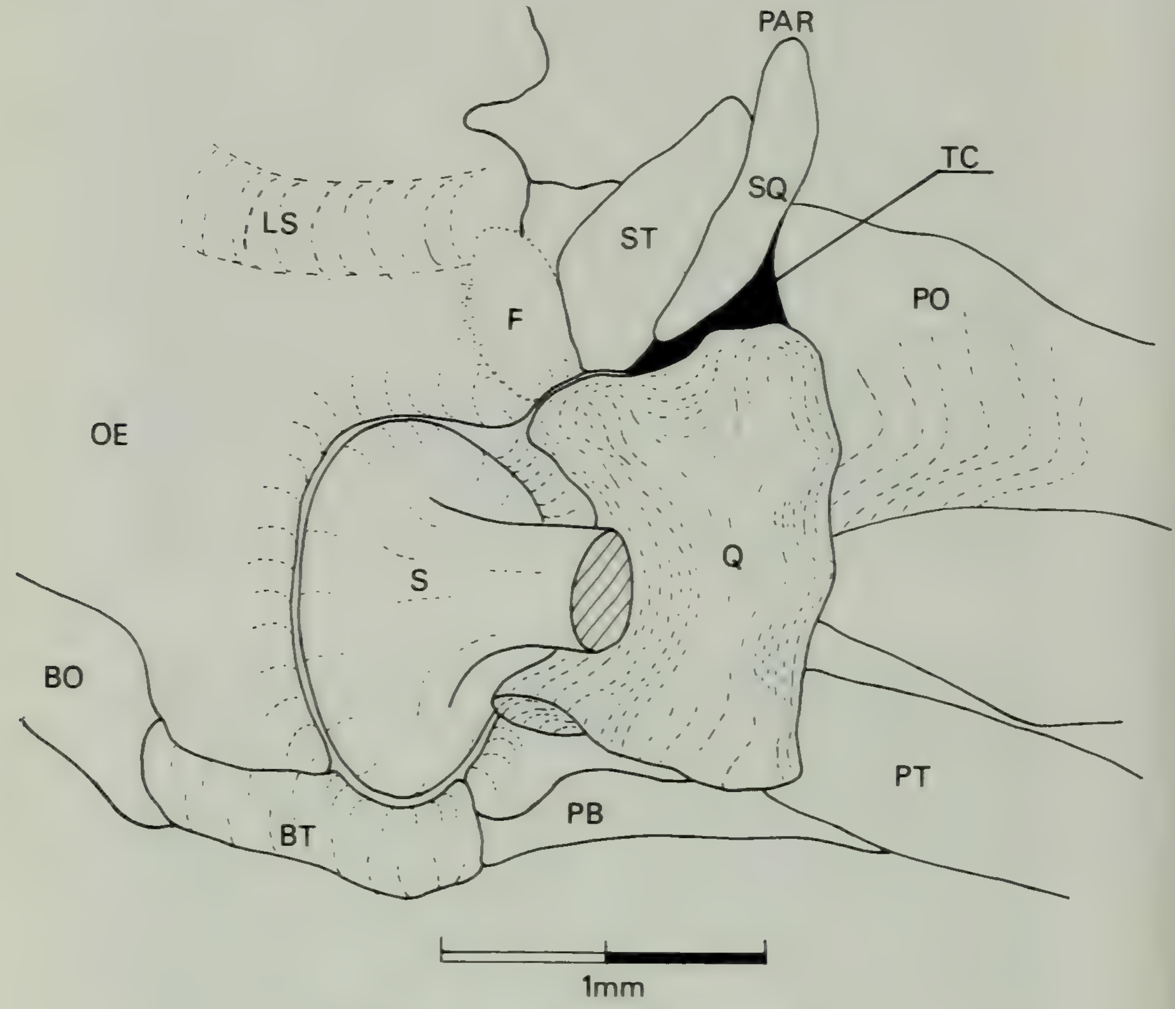

Fig. 3. Posterolateral view of the skull.

The proportions of the posterior half of the skull are of importance. The temporal region, where the adductor musculature is accommodated, is laterally compressed and the otico-occipital region is much expanded both laterally and posteriorly (Figs 1A–B, 2A). These relations create the impression that the suspensorium is more anteriorly located than in a non-fossorial lizard such as *Mabuia*. The entire posterior border of the parietal meets the supraoccipital and the fused exoccipital-opisthotic complex in a dorsally lying suture. There is thus no posttemporal fenestra and the back of the skull is smooth and bluntly rounded (Fig. 1A). Immediately below the foramen magnum a kidney-shaped condyle is present, composed laterally of the exoccipitals and medially of a suturally distinct basioccipital bone. Ventrally the basioccipital forms the posterior portion of the skull base, curving upwards to meet the exoccipital ventrolaterally to the condyle.

A tympanum and middle ear cavity are absent. The columella is massive, consisting of a large footplate and a short anterolaterally directed stapes (Figs 3–4), which extends laterally beyond the quadrate as a rod-like cartilaginous extracolumella, terminating a short distance anterior to the quadrate and ventrolateral to the medius portion of the external adductor muscle (Figs 5, 7–8, 12–13). The tendinous sheath surrounding the extracolumella is joined to the retroarticular process of the lower jaw as in *Typhlosaurus caecus* (Smit 1964) and *Acontias meleagris* (De Villiers 1939; Brock 1941; Van der Merwe 1944), and is suspended anteriorly by a ribbon of fascia overlying the tendinous covering of the adductor musculature and attaching to the dorsolateral border of the parietal (Figs 5, 7–8, 12). The same condition exists in *T. caecus* and *T. lineatus*.

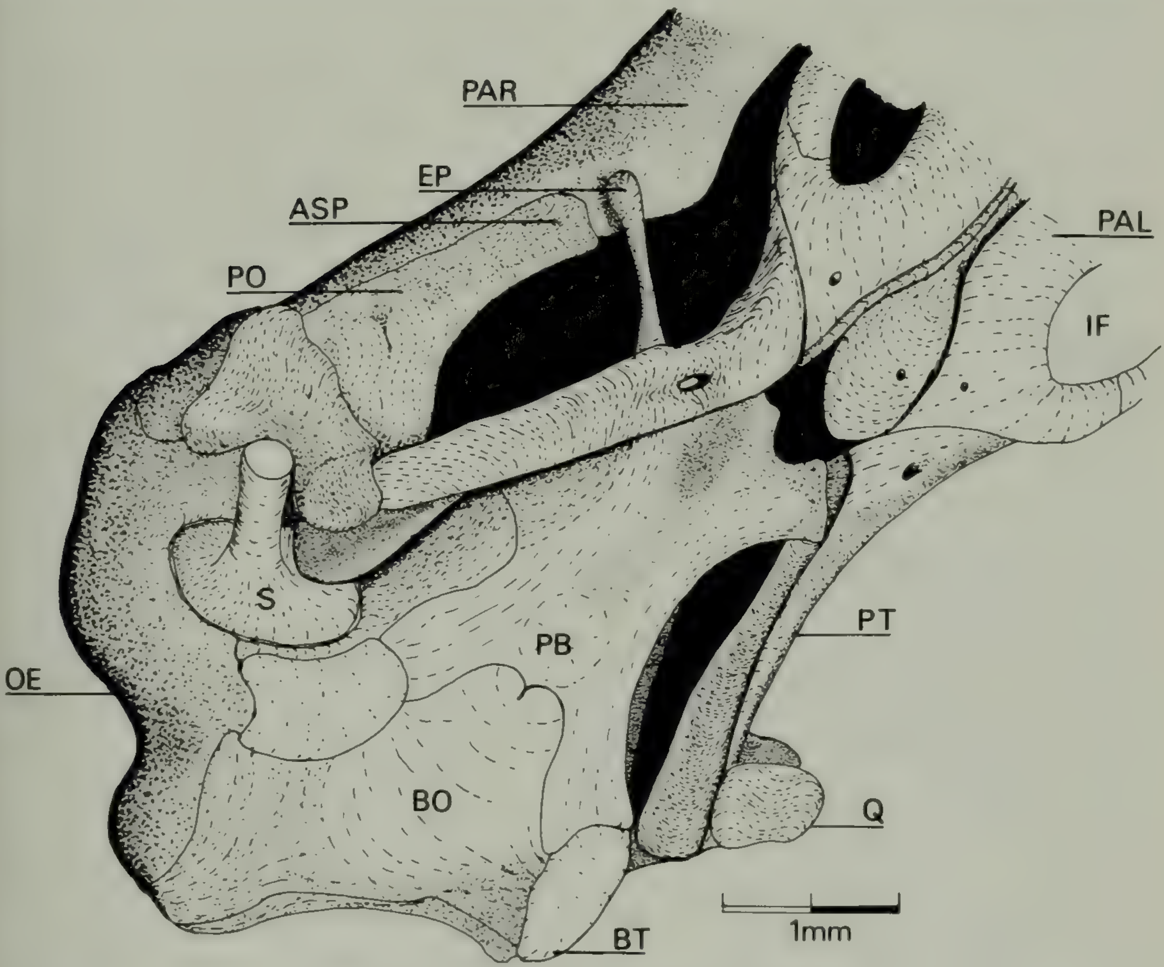

Fig. 4. Posteroventral view of the skull.

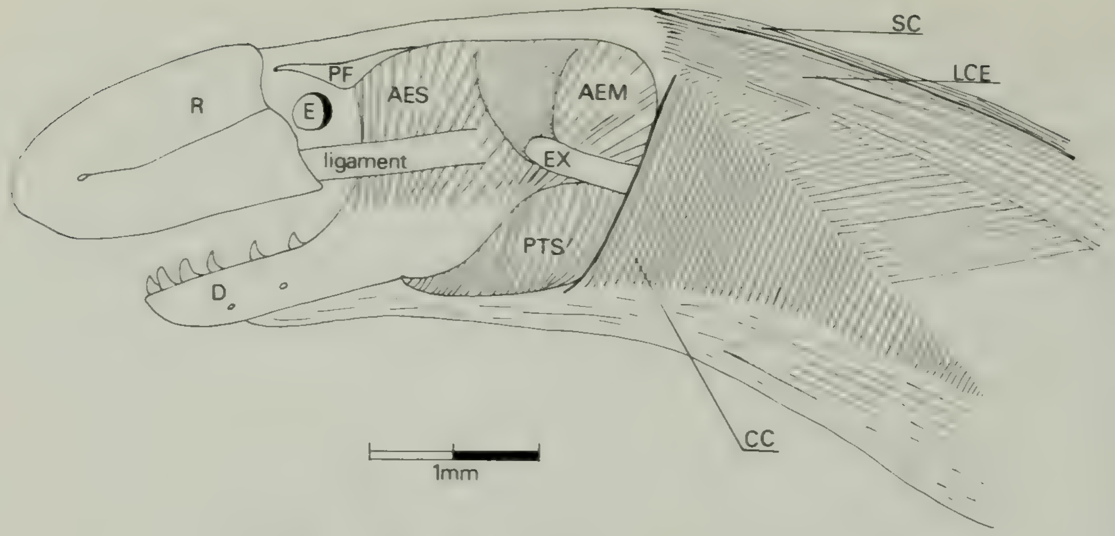

Fig. 5. Lateral superficial view of musculature.

The quadrate ramus of the pterygoid is gutter-shaped, with the trough directed medially in the region of the basipterygoid joint to receive the basipterygoid process. Posteriorly the quadrate ramus is twisted through ninety degrees so that the trough faces ventrally where the posterolateral extremity of the bone is tendinously connected to the ventromedial surface of the quadrate (Fig. 4).

The anterior border of the quadrate is gently rounded for the attachment of the lateral lamina of the quadrate tendon, while the posterior border of the bone is concave to accommodate the laterally protruding stapes (Fig. 3). Ventrally the large quadrate condyle articulates synovially with the lower jaw. Dorsal to the attachment of the quadrate ramus of the pterygoid the medial surface of the quadrate is slightly concave to accommodate the origin of the posterior adductor muscle (Fig. 13). Dorsally the posterior part of the quadrate head articulates synovially with both the supratemporal and the otic capsule (Figs 3, 14).

The anterior part of the quadrate head is separated from the cranium by fibres of the medius portion of the external adductor muscle and serves for the origin of the vertical lamina of the quadrate tendon. The central part of the quadrate head is tendinously attached to the squamosal (Figs 3, 13).

The thin, rod-like epipterygoid fits ventrally into the columellar fossa on the dorsal surface of the pterygoid, lateral to the basipterygoid joint. Both condylar surfaces are capped by cartilage. The dorsal extremity of the bone attaches tendinously to the lateral surface of the parietal downgrowth immediately in front of the anterior superior process of the pro-otic (Fig. 4).

Because of the importance of the mandibular muscle insertions it is necessary to augment the brief description of Smit (1964) of the lower jaw of *Typhlosaurus caecus*. Each ramus consists of the normal six bones, viz. dentary, coronoid, splenial, surangular, angular and a fused articular-prearticular, to which the surangular is also partially fused (Fig. 17). Between the coronoid process and the glenoid fossa both dentary and surangular bulge laterally, forming a dorsolateral mandibular shelf on to which elements of the adductor musculature insert (Fig. 11). Posteriorly, at the insertion of the pterygomandibularis muscle, the ventral border of the jaw is concave (Fig. 17).

The dentary extends from the symphysis to the supra-angular foramen and constitutes the anterior portion of the mandibular shelf (Figs 9–10). It carries eight to nine pleurodont teeth, contributes the lateral half of the coronoid process and is medially recessed along its posterior half to accommodate the remaining lower jaw bones (Fig. 17). It is pierced laterally and antero-ventrally below the tooth row by a line of four mental foramina, and postero-medially by a large foramen transmitting the anterior mylohyoid nerve and the lingual branch of the inferior alveolar nerve; anteromedially there are foramina for the Meckelian cartilage and the anterior tip of the inferior alveolar nerve. The position of the posteromedial foramen varied in the two *Typhlosaurus aurantiacus* specimens investigated. In the serially sectioned skull the anterior process of the coronoid bone and the anterior tip of the splenial form the posterior border of the foramen, whereas, in the cleared specimen, the foramen lies well within the boundaries of the dentary (Fig. 17). Behind the coronoid process, fibres of the posterior adductor muscle and the medius portion of the external adductor muscle insert along the dorsolateral border of the dentary.

The coronoid lies midway along the mandible, flattened medially against the dentary, prearticular and surangular. Its coronoid process is a prominent vertical sheet lying against the coronoid process of the dentary (Figs 2B, 9). Ventrally the bone is braced against the action of the adductor muscles by an anterior and a posterior process, the former bridging the dentary-prearticular suture and the latter the surangular-prearticular suture (Fig. 17). Two parallel, near-vertical grooves are present on the trailing edge of the coronoid process. Separated by a ridge, they continue posteroventrally on to the medial side of the posterior process; the more lateral of the two grooves receives the insertion of the medius portion of the external adductor muscle while the pseudotemporalis muscle inserts into the medial groove (Figs 10, 17).

The surangular (Figs 9–12, 17) lies posteromedially to the dentary, posterolaterally to the coronoid, dorsally to the prearticular and anteriorly to the articular. Laterally it forms the posterior section of the mandibular shelf (Fig. 11) and dorsally it bears a ridge extending between the coronoid and the articular processes. Its anterior extremity underlies the coronoid process while in addition to covering the Meckelian canal up to the adductor fossa, the posterodorsal tip of the bone constitutes the anterior part of the articular process. Posteromedially the bone forms the dorsal border of the adductor fossa and is laterally pierced by the posterior supra-angular foramen, which leads from the adductor fossa, and the anterior supra-angular foramen which leads from the Meckelian canal. The posterior adductor muscle and medius portion of the external adductor muscle insert on the dorsomedial and dorso-

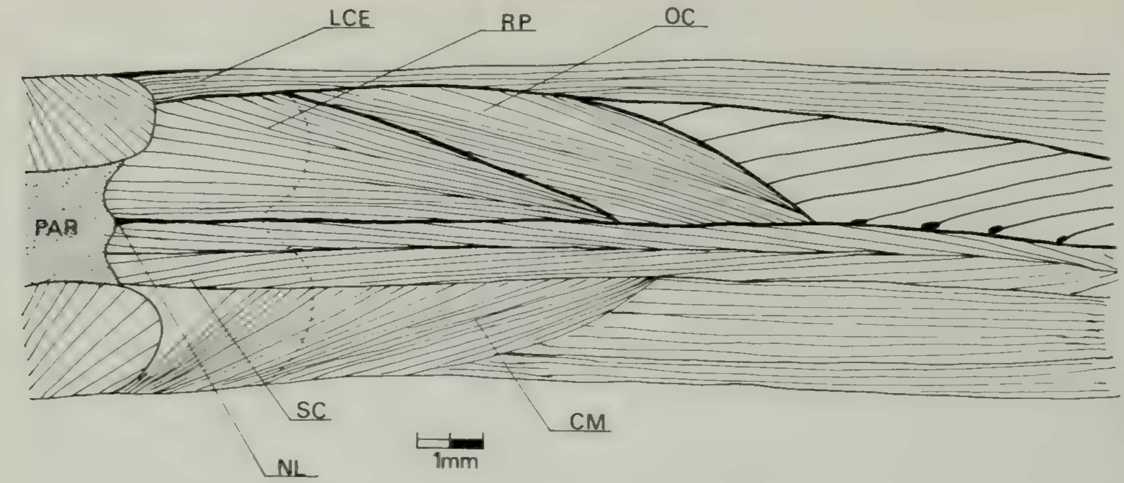

Fig. 6. Dorsal superficial view of the cervical musculature; spinalis capitis muscle removed on the right side.

lateral surfaces of the surangular. Posteriorly the bone is fused to the articular-prearticular complex.

The splenial (Figs 9–10) is a thin sliver of bone on the inner surface of the jaw in line with the coronoid process. It lies posteromedially to the dentary, medially to the prearticular, dorsally to the angular and ventrally to the coronoid. It is devoid of any muscle insertions and neither bears foramina nor contributes to the inner wall of the Meckelian canal.

The angular (Figs 9–10, 11, 17), a narrow ventral element below the prearticular and splenial, lies with its anterior tip within the dental recess and traverses the jaw posteroventrally between the prearticular and dentary to terminate posteriorly on the lateral surface of the mandible, ventral to the posterior tip of the surangular. Between the prearticular and dentary it forms a narrow medial section of the floor of the Meckelian canal, from the adductor fossa to immediately anterior to the coronoid process. At its midpoint it is pierced ventrally by the posterior mylohyoid foramen, which transmits the posterior mylohyoid nerve.

The prearticular (Figs 11–12, 17) lies ventrally to the surangular, posteromedially to the dentary, dorsally to the angular and laterally to the coronoid and the splenial. It forms most of the medial wall and part of the floor of the Meckelian canal as well as the ventral border of the adductor fossa. Medially it receives the insertion of the adductor musculature and posteriorly it is completely fused to the articular.

Behind the glenoid fossa the articular-prearticular (Figs 13–17) forms the spoon-shaped retroarticular process, which receives the insertion of the pterygoideus muscle on its medial and lateral surfaces and that of the depressor mandibulae muscle on the dorsal surface. The glenoid fossa, lined with cartilage, lies in front of the insertion of the depressor mandibulae muscle and behind and against the articular process. The foramen for the chorda tympani lies medially on the retroarticular process, with its canal extending anteriorly through the bone to open into the adductor fossa.

The hyoid apparatus in *Typhlosaurus aurantiacus* is a triradiate, cartilaginous structure resembling a tuning-fork with posteriorly divergent prongs. It lies ventral to the trachea and extends posteriorly from the glottis to a point in line with the posterior border of the pterygoideus muscle. Anteriorly, in the ventral midline, the lingual process (proc. entoglossus) supports the tongue musculature (Figs 9–10).

No part of the hyoid apparatus is ossified and the structure could consequently not be divided with certainty into the various components commonly found in reptiles. From the work of Van der Merwe (1944), Langebartel (1968) and De Weerdt (1971) it appears that the paired posterior prongs represent the first ceratobranchials.

Cervical osteology

Vertebrae and ribs are highly variable structures and in the limbless squamates the regional differentiation of the vertebral column has lead to various interpretations of the cervical vertebrate. Zangerl (1945) recognizes four vertebral divisions in the Amphisbaenidae, i.e. cervical, thoraco-lumbar, cloacal and caudal. The cervical region includes all the anterior ribless vertebrae, i.e. atlas, axis and one to two of the following vertebrae, whilst the thoraco-lumbar region includes all vertebrae with movable unforked ribs. Sood (1948) divides the ophidian vertebral column into a precaudal and a caudal region of which the former is subdivided into cervical, thoracic and lumbar subregions. The cervical sub-region consists only of the atlas and the axis whereas the thoracic region includes all vertebrae following the axis and which bear hypapophyses. List's (1966) description of the burrowing snakes follows Zangerl (1945) in defining the regions of the vertebral column. Consequently he defines the cervical region in burrowing snakes as consisting only of the atlas and the axis since the vertebrae following the axis bear unforked ribs and are therefore included in the thoraco-lumbar region. List notes that although this system appears satisfactory for the Typhlopidae and Leptotyphlopidae its use is limited in that it cannot be directly applied to other vertebrates.

According to Gasc (1968) and Hofstetter & Gasc (1969) the cervical vertebrae can only be defined as those vertebrae preceding the vertebrae carrying the first rib attached to the sternum. These authors refer to the work of Stannius (1849) and state that all other definitions of cervical vertebrae such as ribless anterior vertebrae, vertebrae with hypapophyses or ribless vertebrae plus vertebrae with short ribs are invalid because too many exceptions and contradictions are involved.

Limb regression is usually accompanied by regression of the girdles and in certain of the fossorial Scincidae, e.g. in the genus *Typhlosaurus*, this phenomenon is rather pronounced. In *Feylinia* the ribs of the eighth vertebra are still attached to a vestigial sternum (Gasc 1965), in *Dibamus* the pectoral girdle is connected to the fifth vertebra (Gasc 1968) and in *Acontias meleagris* the

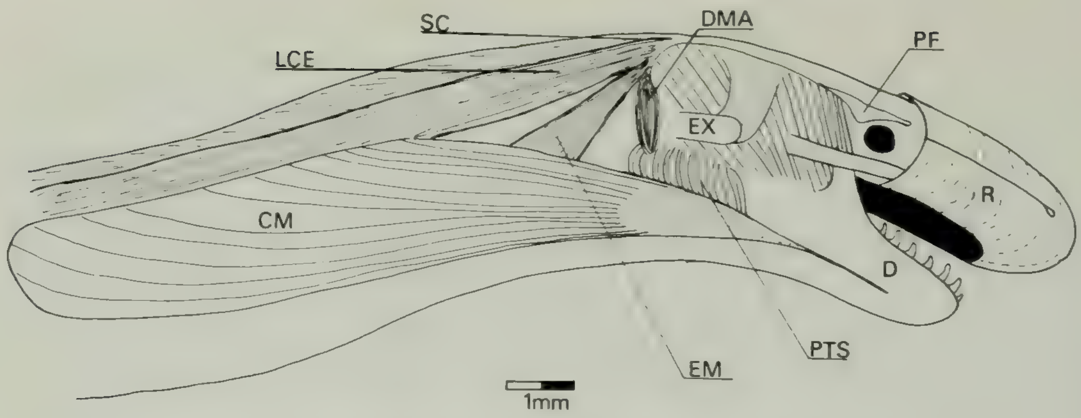

Fig. 7. Ventrolateral view of the superficial neck musculature.

vestigial girdle is united by the serratus muscle to the second and the third ribs. In *T. vermis* the pectoral girdle is absent (Hofstetter & Gasc 1969). In *T. aurantiacus* the pectoral girdle is also absent, and the ribs consequently lack sternal attachments. It is therefore not possible to define a specific cervical region within the vertebral column of *T. aurantiacus*. In limbless squamates such as ophidians (completely lacking a pectoral girdle) and amphisbaenids (lacking sternal attachments of the ribs) Hofstetter & Gasc (1969) divide the vertebral column into precloacal, cloacal and caudal regions.

In this paper the term 'cervical' does not define a region of the vertebral column but refers only to that area on the precloacal region of the vertebral column from which the musculature responsible for the movements of the head arise.

Typhlosaurus aurantiacus has procoelous vertebrae as in all saurians except the Gekkonidae. The broad elliptical condyles are slightly dorsally orientated and are as wide as the centra of the vertebrae. The first pairs of ribs are carried by the third vertebra, as in *Acontias meleagris*.

The ribs are holocephalous (unicipital) and each has two tuberculiform processes close to the costal head; one anteroventrally and one posterodorsally for the attachment of the intercostal muscles. A similar condition exists in *T. vermis* (Hofstetter & Gasc 1969). As a result of the increased functional importance of the cervical musculature in a limbless burrower such as *T. aurantiacus*, the synapophysis of the axis and the following three vertebrae are laterally extended to enlarge the area of origin of the cervical musculature.

The atlas consists of paired neural arches and a ventral intercentrum. A neural spine is absent and the two semilunate neural arches do not fuse dorsally. No functional zygapophyses are present between the atlas and the axis, although the atlas has a small process on the posterolateral margin of the neural arch in a similar position to the postzygapophyses of the other vertebrae.

The axial centrum bears two hypapophyses, of which the posterior one is probably derived from the intercentrum of the third vertebra as Holder (1960) found in gekkos. Anterolaterally the neural arch has a small process coinciding with the position of the prezygapophyses on the vertebrae following the axis. The neural spine resembles the blade of an axe and extends the full length of the neural arch.

Midventrally on the centra of each of the seven vertebrae following the axis a hypapophysis is present. The neural spines, posterodorsally situated on the neural arches, extend obliquely caudally. The vertebrae articulate by means of pre- and post-zygapophyseal processes and no zygosphene-zygantrum type of articulation, as found in snakes and some saurian families, is present in *Typhlosaurus aurantiacus*.

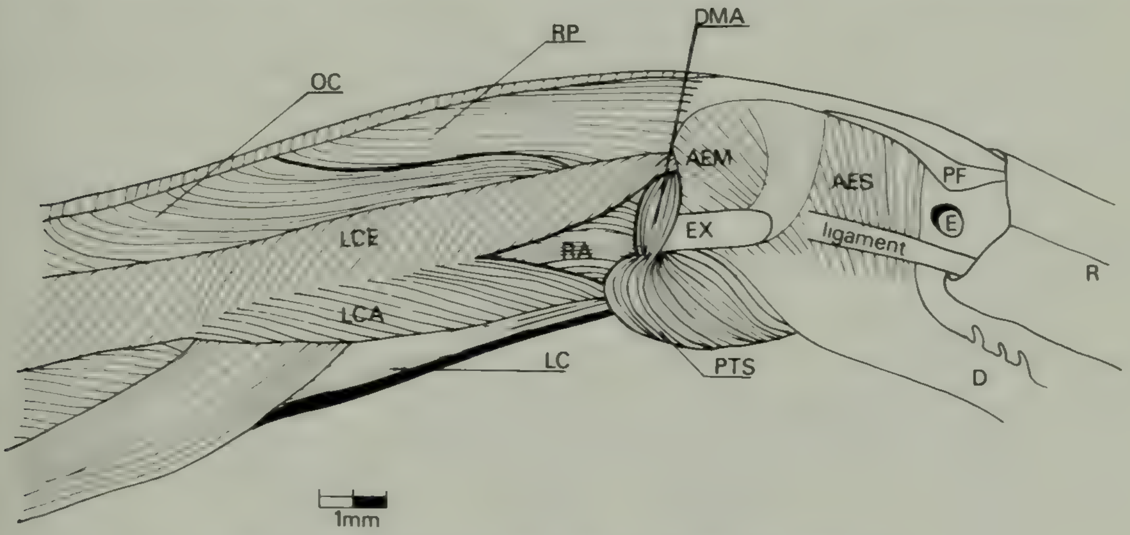

Fig. 8. Lateral view of the deep cervical musculature.

MYOLOGY

Muscle classification and nomenclature

The currently accepted classification of visceral cranial muscles is based on Vetter's (1874, 1878) and Ruge's (1897) studies on selachians. The Constrictor superficialis (Cs) is subdivided into segmentally innervated portions, i.e. the trigeminus muscle complex as the Constrictor superficialis I (Cs_1); the facial muscles as the Constrictor superficialis II (Cs_2); the glossopharyngeal muscles as the Constrictor superficialis III (Cs_3); and the vagus muscles as the Constrictor superficialis IV–VIII (Cs_{4-8}). Luther (1914) extended this classification to tetrapods and introduced a subdivision of the jaw adductors based on the spatial relationships of the muscles with the three rami of the trigeminal nerve. This system has been generally accepted for sauropsids by most authors including Adams (1919), Lakjer (1926), Haas (1930, 1934, 1973), Lubosch (1933), Edgeworth (1935), Brock (1941), Säve-Söderbergh (1945), Ingeborg Poglayen-Neuwall (1953, 1954), Ivo Poglayen-Neuwall (1953*a*, 1953*b*), Oelrich (1956), Ostrom (1961), Gasc (1968) and Barghusen (1973). In sauropsids the Constrictor I is divided into the m. constrictor I dorsalis ($M.C_1d$), the m. constrictor I lateralis ($M.C_1l$) represented by the m. adductor mandibulae, and a m. constrictor I ventralis ($M.C_1v$), the m. intermandibularis.

The constrictor I dorsalis ($M.C_1d$) extends between the cranium and the movable palatal complex. This group of muscles is involved with kinetic movements of the skull and they are variable in their occurrence.

Basically, the constrictor I lateralis ($M.C_1l$), the m. adductor mandibulae of sauropsids, is divided into an external, and internal and a posterior muscle. The external adductor is usually subdivided into three portions, i.e. superficialis, medius and profundus. The internal adductor commonly consists of two, well-separated muscles, the m. pseudotemporalis and the m. pterygoideus. The posterior adductor is usually a single muscle.

The constrictor I ventralis ($M.C_1v$), the m. intermandibularis, is situated between the rami of the lower jaws, superficial to the throat musculature, and is subdivided into an anterior and a posterior portion.

Lubosch (1933) recongizes three basic arrangements of jaw muscles, i.e. selachian, amphibian and mammalian, of which the jaw muscles of sauropsids belong to the amphibian type. Homologies between the three types are uncertain, according to Haas (1973), and are further complicated by the varied nomenclature in existence for saurian jaw musculature. For a complete list of synonyms see Lakjer (1926), Edgeworth (1935) and Haas (1973).

Nishi (1919) laid down the terminology for axial musculature and, together with Vallois (1922), is amongst the few workers who have approached axial musculature on a comparative basis. More recent accounts are those of Olson (1936) and Evans (1939).

Reptilian epaxial musculature is divisible into three longitudinal systems. Dorsomedially the transversospinalis system lies lateral to the spinous processes of the vertebrae, the longissimus system lies lateral to the transversospinalis system and dorsal to the heads of the ribs, and the iliocostalis system lies on the ribs dorsal to the upper margin of the external oblique abdominal muscles. Anteriorly, towards the occiput, the epaxial musculature breaks down into various shorter groups of fibres, the cervical muscles, which insert posteriorly on to the skull and are responsible for the movements of the head.

The hypaxial musculature does not fall within the scope of this paper.

Constrictor dorsalis group (C_1d)

This group of muscles lies deep to the adductor musculature and is responsible for the intercranial kinetic movements of the skull. The muscles arise, in Versluys' (1912) terminology, on the occipital segment of the skull and insert on to the maxillary segment. In *Typhlosaurus aurantiacus* the group is represented by a minute m. levator pterygoidei and a large m. protractor pterygoidei. A levator bulbi muscle is absent.

The small m. levator pterygoidei (lp, Figs 9–10), roughly triangular in transverse section, lies laterally to the basipterygoid joint, the opthalmic ramus of the trigeminal nerve, the palatine ramus of the facial nerve, the internal

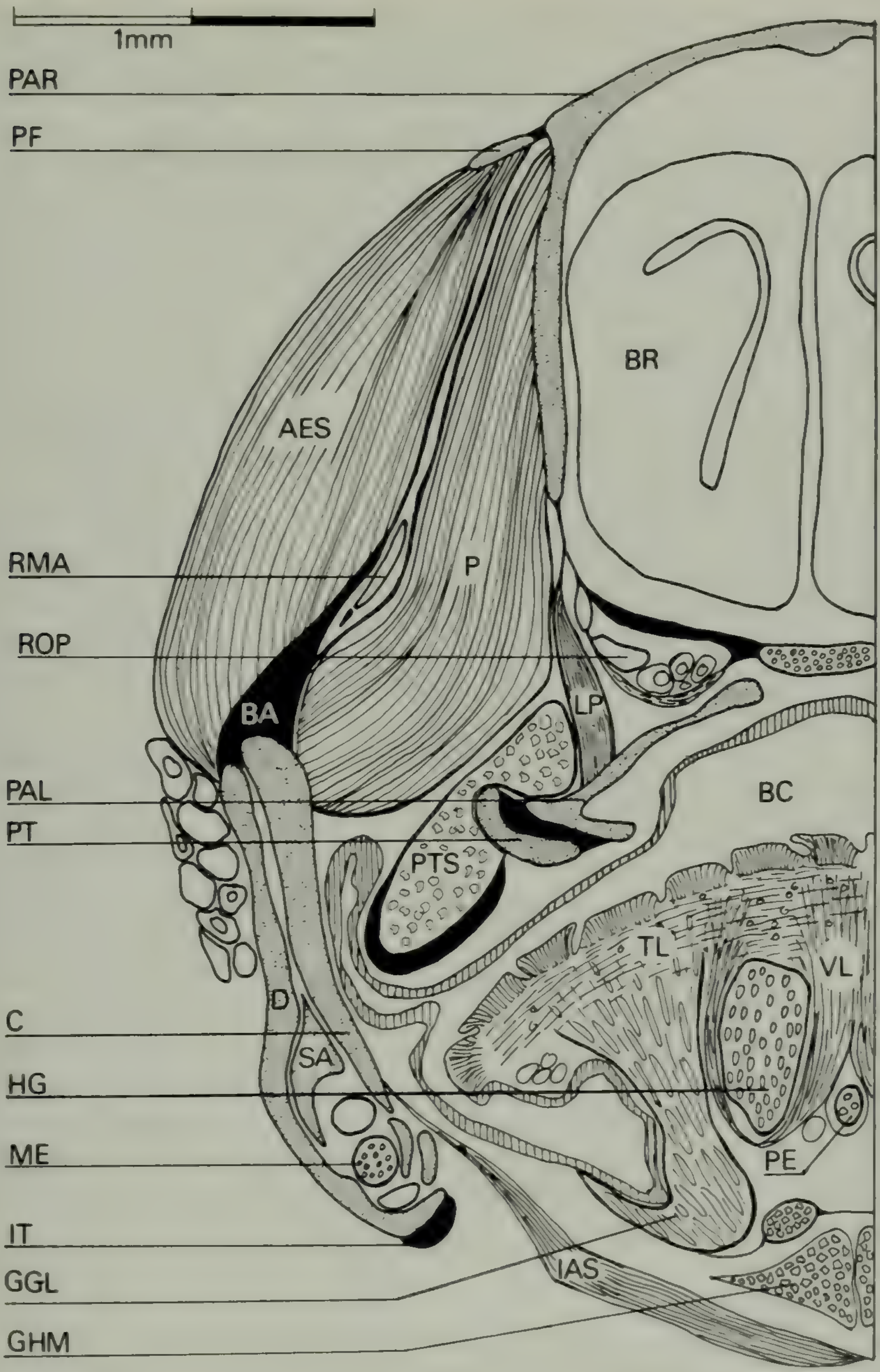

Fig. 9. Cross-section of the skull at the level of the coronoid process.

carotid artery and the origin of the protractor pterygoidei muscle; medially to the pseudotemporalis muscle, the anterior part of the pterygoideus muscle and the epipterygoid. It lies against the medial surface of the epipterygoid with the posterior border of the muscle in line with that of the bone.

The muscle arises as a ribbon of fascia from the lateral surface of the pro-otic membrane, ventral to the lateral parietal downgrowth, medioventral to the dorsal extremity of the epipterygoid bone and anteroventral to the anterior superior process of the pro-otic.

The insertion is fleshy and bridges the palatine-pterygoid suture dorsally. Anteriorly it attaches on to the posterolateral border of the palatine bone, medially to the anterior extremity of the pterygoideus muscle, and posteriorly it attaches on to the anterodorsal surface of the pterygoid bone medially to the columellar fossa.

A nerve seen within the muscle in transverse section was too small for its connections to be traced.

The large m. protractor pterygoidei (prp, Figs 11–14) lies behind the the basipterygoid process, the individual fibres extending obliquely between the lateral margin of the skull base and the full length of the quadrate ramus of the pterygoid. The muscle is situated posteromedially to the levator pterygoidei muscle, medially to the mandibular ramus of V, dorsally to the pterygoideus muscle, ventrally to the Gasserian ganglion and the proximal part of the opthalmic ramus, and laterally to the parasphenoid-basisphenoid complex, the otic capsule, the palatine ramus of VII, and the internal carotid artery.

The muscle arises fleshily from the dorsal surface of the basipterygoid process, the lateral surfaces of the parasphenoid-basisphenoid complex and the anterior inferior process of the pro-otic, and anteroventrally from the lateral surface of the pro-otic proper (Figs 9–11). Anteroventrally within the muscle a flat tendon is present which arises ventrally on the basipterygoid process. Fibres arise from both dorsal and ventral surfaces of the tendon.

The insertion is confined to the quadrate ramus of the pterygoid bone posterior to the basipterygoid process. Fibres insert along the inner concave surface and the dorsal surface of the ramus. An insertional tendon is present within the muscle, posterodorsally to the tendon of origin, the fibres insert on to its dorsal and ventral surfaces. This tendon attaches to the dorsal (inner) rim of the quadrate ramus (Figs 11–12).

The muscle is innervated by a separate branch of V leaving the Gasserian ganglion ventrally, piercing the muscle dorsally and coursing anteriorly a short distance before ramifying.

Adductor mandibulae group

Compared with non-fossorial lizards, the adductor musculature as exemplified by *Typhlosaurus aurantiacus* is modified to function as a compact unit within the temporal indentation. The external adductors are dominated by two oblique, parallel tendons, of which the anterodorsal one is a modified bodenaponeurosis. It arises as a single tendon on the coronoid process of the lower jaw (Fig. 9), posterior to which it fans out into the external adductor mass as three laminae. In transverse section this unit appears as a tripartite structure resembling an inverted Y (Fig. 11). The three laminae serve as areas of insertion to the external and internal adductors and will be referred to in the text as the vertical, medial and lateral laminae of the bodenaponeurosis.

The second tendon (Figs 11–12), located posteroventrally to the bodenaponeurosis, also shows a tripartite configuration. It arises on the quadrate and extends anteroventrally to just posterior to the base of the coronoid process. This tendon will be referred to as the quadrate tendon and its laminae as the vertical, medial and lateral laminae of the quadrate tendon. Each lamina has a separate origin from the quadrate. The vertical lamina arises from the dorsal midline of the quadrate, piercing the medius portion of the external adductor muscle ventromedially. The lateral lamina arises from the anterior border of the bone and the medial lamina along its inner dorsal surface (Fig. 13), covering the medial surface of the posterior adductor fibres arising from the medial surface of the quadrate.

Ventrolaterally to the superficial portion of the external adductor and anteromedially to the extracolumella, a ligament is present in the position of the quadrato-maxillary ligament as described by Ingeborg Poglayen-Neuwall (1953) and Haas (1960). In *Typhlosaurus aurantiacus*, however, this ligament arises ventrolaterally from the lateral lamina of the bodenaponeurosis and extends anteriorly within the upper lip (Figs 5, 7–8), terminating laterally to the premaxillary. Ventrolaterally to the orbit the integument turns under this ligament to form the angle of the mouth.

A small horizontal bundle of muscle fibres is associated with the extracolumella (Fig. 12). It lies in a somewhat similar position to the m. retractor anguli oris of the amphisbaenids *Amphisbaena* and *Leposternon* as described by Lakjer (1926). However, in *Typhlosaurus aurantiacus* these fibres extend between the anteromedial surface of the extracolumella and the lateral lamina of the bodenaponeurosis and they apparently function to draw the extracolumella against the lateral surface of the adductor musculature.

The three major divisions of the adductor mandibulae group are readily identified by virtue or their spatial relationship with the three rami of the trigeminal nerve (Luther 1914). In *Typhlosaurus aurantiacus* the external adductor muscle mass lies laterally to the maxillary and mandibular rami (Figs 10–12), the internal adductor lies medially to the maxillary but laterally to the ophthalmic rami (Fig. 9), and the adductor posterior lies laterally to the mandibular ramus and ventrally to the external adductor (Fig. 12).

Musculus adductor mandibulae externus

The external adductor musculature arises within the temporal indentation and its origin is bordered dorsally by a curved ridge on the parietal, extending from the posterior tip of the postfrontal to the posterior extremity of the parietal (Figs 9–14).

Three portions of the external adductor musculature—the superficialis, medius and profundus—are present, either separated by tendinous laminae or by differences in fibre orientation.

The musculus adductor mandibulae externus superficialis (aes, Figs 9–11), the most lateral portion of the external adductor, lies partially anterior to the medius and profundus portions. Posteriorly, it is separated from them by, respec-

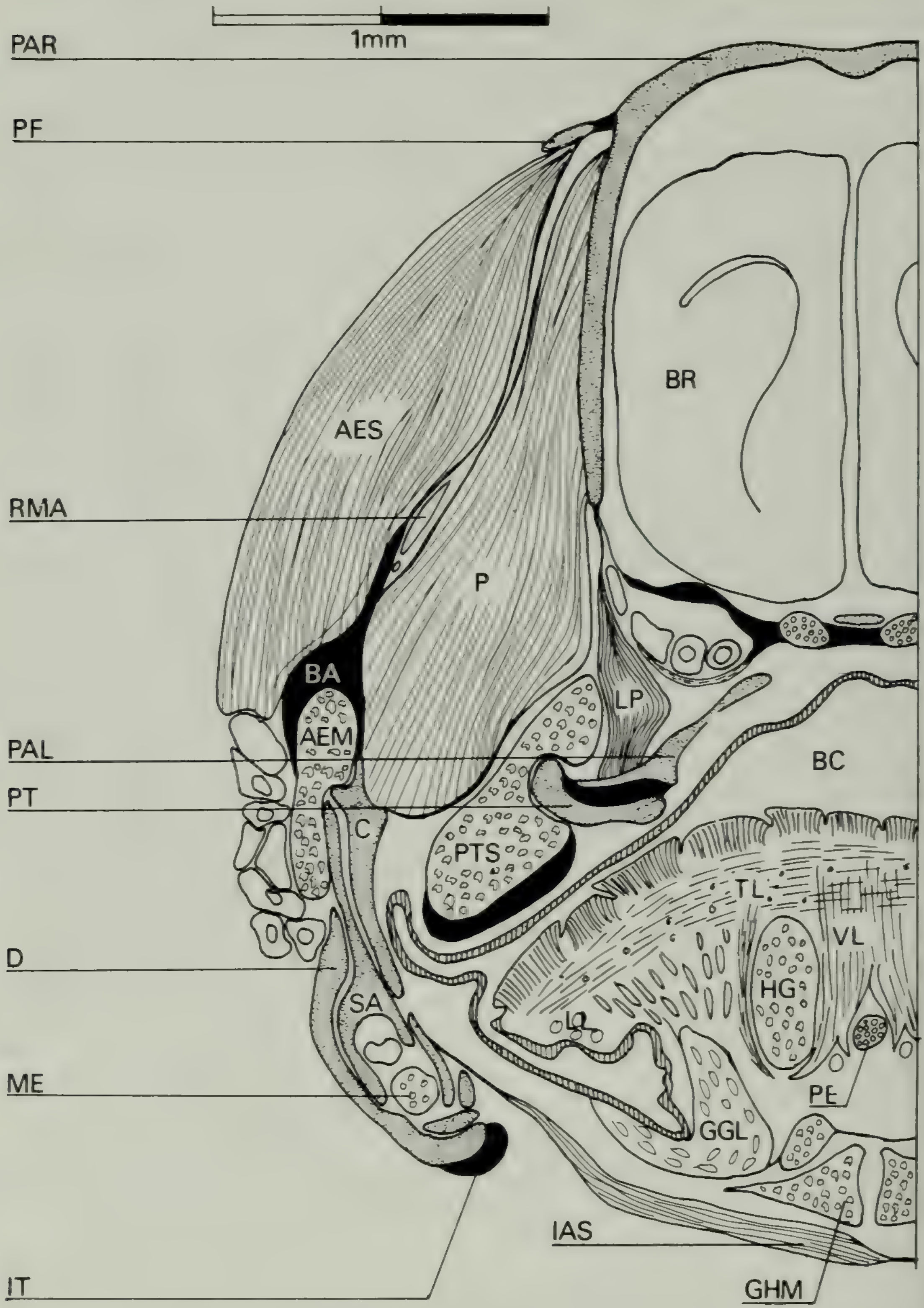

Fig. 10. Cross-section of the skull just behind Figure 9.

tively, the lateral and the vertical laminae of the bodenaponeurosis. Anteriorly the superficialis lies lateral to the pseudotemporalis muscle and is separated from it by the maxillary ramus of the trigeminal nerve. Dorsal to the vertical lamina of the bodenaponeurosis there is no distinction, other than fibre orientation, between the superficialis and profundus portions. The superficialis, however, is readily identified by the dorsoventral arrangement of its fibres as opposed to the anteroventral orientation of the profundus fibres. The two portions are by no means confluent since they separate easily during dissection. The most substantial part of the superficialis lies dorsal to the coronoid process, resulting in a near vertical fibre orientation relative to the long axis of the lower jaw (Fig. 9).

The superficialis portion arises from the ventral surface of the postfrontal (Fig. 9), from the dorsolateral ridge on the parietal (Fig. 11) and from the lateral surface of the profundus portion. The origins are fleshy throughout.

Insertion is effected laterally on to the vertical and lateral laminae of the bodenaponeurosis (Fig. 9), from the coronoid process posteriorly to a point dorsal to and almost in line with the anterior tip of the extracolumella.

The superficialis portion is innervated by a posterolateral branch of the mandibular ramus of V, which runs anterodorsally through the medius portion to enter the medial surface of the superficialis portion via the medial lamina of the bodenaponeurosis.

The musculus adductor mandibulae externus medius (aem, Figs 11–14) lies posterolaterally to the pseudotemporalis muscle and between the bodenaponeurosis and the quadrate tendon, with the vertical lamina of the latter piercing it along the ventromedial border. It extends anteroventrally from the posterolateral border of the parietal to the lower jaw and, being the most ventral portion of the external adductor muscle, its dorsal border is wedged between the lower extremities of the superficialis and profundus portions, separated from them by, respectively, the lateral and medial laminae of the bodenaponeurosis. Ventrally the muscle is forked, straddling the lower jaw from the coronoid process to the anterior border of the posterior adductor muscle. At this point there is, for a short distance, no partition between the fibres of the medius portion of the external adductor and those of the posterior adductor (Fig. 11). However, the medius portion is distinctly separated from the posterior adductor by the lateral and medial laminae of the quadrate tendon over practically its entire length. Posterior to the bodenaponeurosis and dorsal to the quadrate, the medius fibres are continuous with those of the more medially situated profundus portion of the external adductor (Fig. 12). It can, however, be determined with reasonable accuracy that most of the fibres in this area belong to the medius portion.

The medius portion arises fleshily from the posterolateral surface of the parietal (Fig. 12), the lateral surfaces of the supratemporal, the squamosal, the pro-otic dorsal to the quadrate and the lateral surface of the quadrate above the extracolumella (Fig. 13).

The insertion remains fleshy throughout and the fibres attach on to the inferior surfaces of the medial and lateral laminae of the bodenaponeurosis, the superior surfaces of the medial and lateral laminae of the quadrate tendon, the medial and lateral surfaces of the vertical lamina of the quadrate tendon, and into

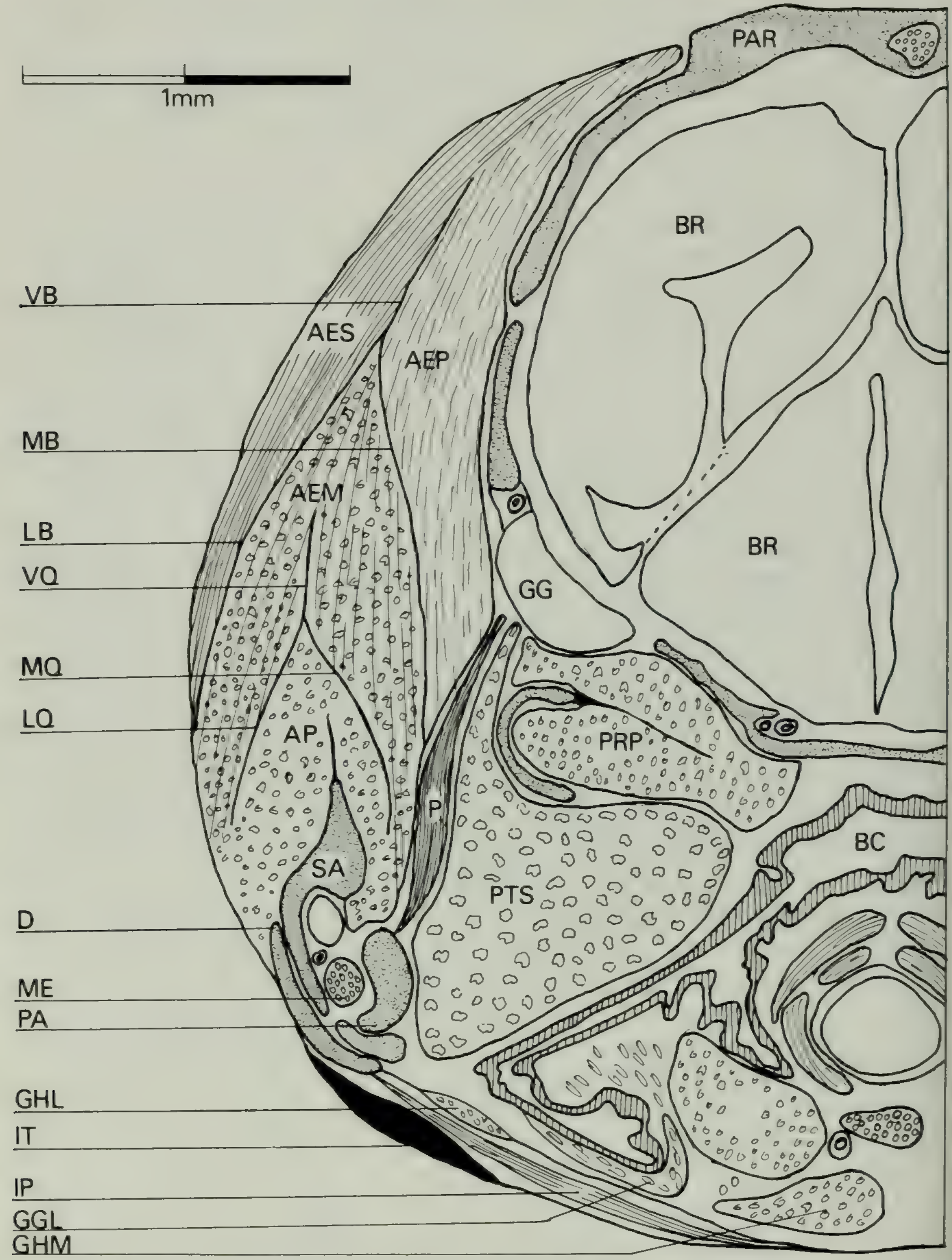

Fig. 11. Cross-section of the skull at the level of the Gasserian ganglion.

the lateral groove on the coronoid (Fig. 10), with a few fibres attaching posterolaterally on to the coronoid process of the dentary. Between the base of the coronoid process and the foramen for the anterior supra-angular nerve, the insertion utilizes the medial surface of the surangular, the dorsomedial surface of the posterior process of the coronoid and a small dorsomedial area on the prearticular, anterior to the adductor fossa. Dorsally the insertion continues along the surangular ridge, anterior to the adductor fossa, as well as along the dorso-lateral surface of the surangular and the dentary forming the mandibular shelf. The diffuse nature of a small posterior part of the insertion has been mentioned.

The medius portion is innervated by a posterolateral branch of the mandibular ramus of V piercing the muscle medially.

The musculus adductor mandibulae externus profundus (aep, Figs 11–12), deepest portion of the external adductor, lies against the lateral cranial wall laterally to the Gasserian ganglion and the maxillary ramus of the trigeminal nerve, posterolaterally to the pseudotemporalis muscle, and medially to the superficial and medius portions of the external adductor.

Extending anteroventrally, the profundus portion arises fleshily behind the postfrontal, on the lateral surfaces of the parietal downgrowth and the anterior superior process of the pro-otic (Fig. 11), as well as anterolaterally on the pro-otic proper (Fig. 12). The area of origin is bounded dorsally by the dorsolateral ridge of the parietal.

This muscle has no direct contact with the lower jaw and inserts fleshily along the entire medial surface of the vertical lamina, and along the dorsal half of the upper surface of the medial lamina of the bodenaponeurosis (Fig. 11). Dorsally to the vertical lamina of the bodenaponeurosis no partition exists between the superficial and profundus muscles (although the latter remains discrete owing to the oblique orientation of its fibres, as opposed to the near vertical orientation of the superficial fibres) (Fig. 11), whereas posterior to the bodenaponeurosis no distinction is apparent between the profundus and medius muscles (Fig. 12). However, the extent of each portion may be fairly easily determined.

The profundus portion is innervated by a branch leaving the mandibular ramus of V immediately below the Gasserian ganglion and turning dorsally for a short distance to enter the muscle medially.

Musculus adductor mandibulae posterior

The posterior division of the adductor mandibulae group is present as a single muscle, the musculus adductor mandibulae posterior (ap, Figs 11–13). It extends anteroventrally from the quadrate to the mandible and lies laterally to the mandibular ramus of the trigeminal nerve and medially to the extracolumella (Fig. 12). It is straddled over its entire length by the medius portion of the external adductor, although separated from it by the lateral and medial laminae of the quadrate tendon (Fig. 11).

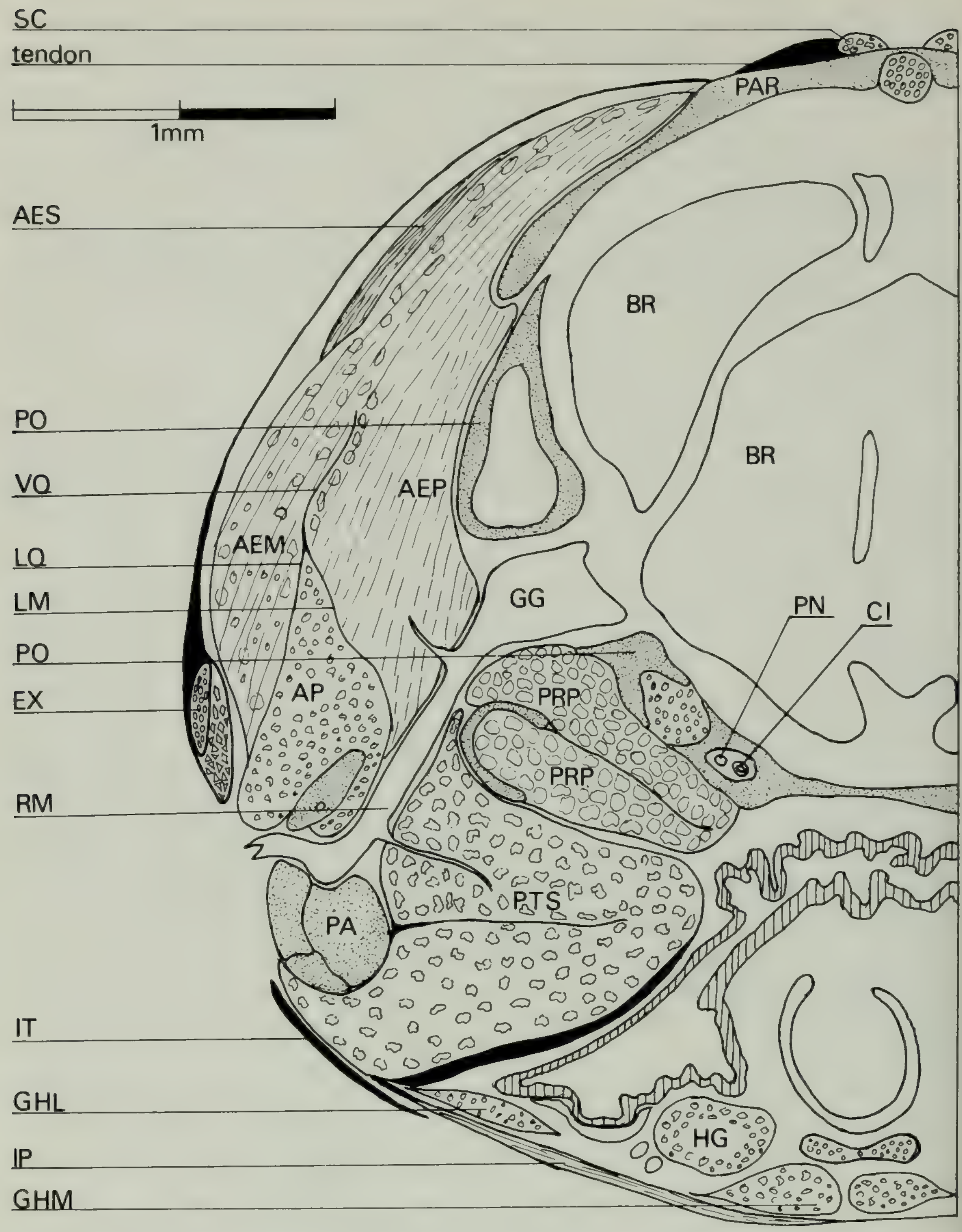

Fig. 12. Cross-section of the skull at the level of the mandibular ramus of V.

The muscle arises fleshily from the slightly concave medial surface of the quadrate, dorsomedially to and in line with the jaw articulation, as well as dorsally to the posterior extremity of the protractor pterygoideus muscle and the attachment of the quadrate ramus of the pterygoid (Fig. 13). The origin is also ventrolateral to the pro-otic and anterior to the stapes, with a few of the most dorsal fibres arising dorsally to the stapes (Fig. 14). Fibres also arise from the anterior border of the quadrate. The quadrate tendon covers the posterior adductor completely (Fig. 12) except at the anterior extremity of the muscle in the region of the anterior supra-angular foramen where, over a short distance, the fibres of the posterior adductor are continuous with those of the medius portion of the external adductor. However, apart from obscuring the exact anterior border of the insertion, this is of little importance since the muscles are effectively separated, in practice, by the quadrate tendon. In addition, some of the posterior adductor fibres arise from the inferior surfaces of the lateral and medial laminae of the quadrate tendon.

The muscle inserts fleshily on to the mandible in an area extending from the articular facet to the base of the coronoid process. Its posterior extremity is pierced ventromedially by a small, robust tendon (Fig. 13), receiving the

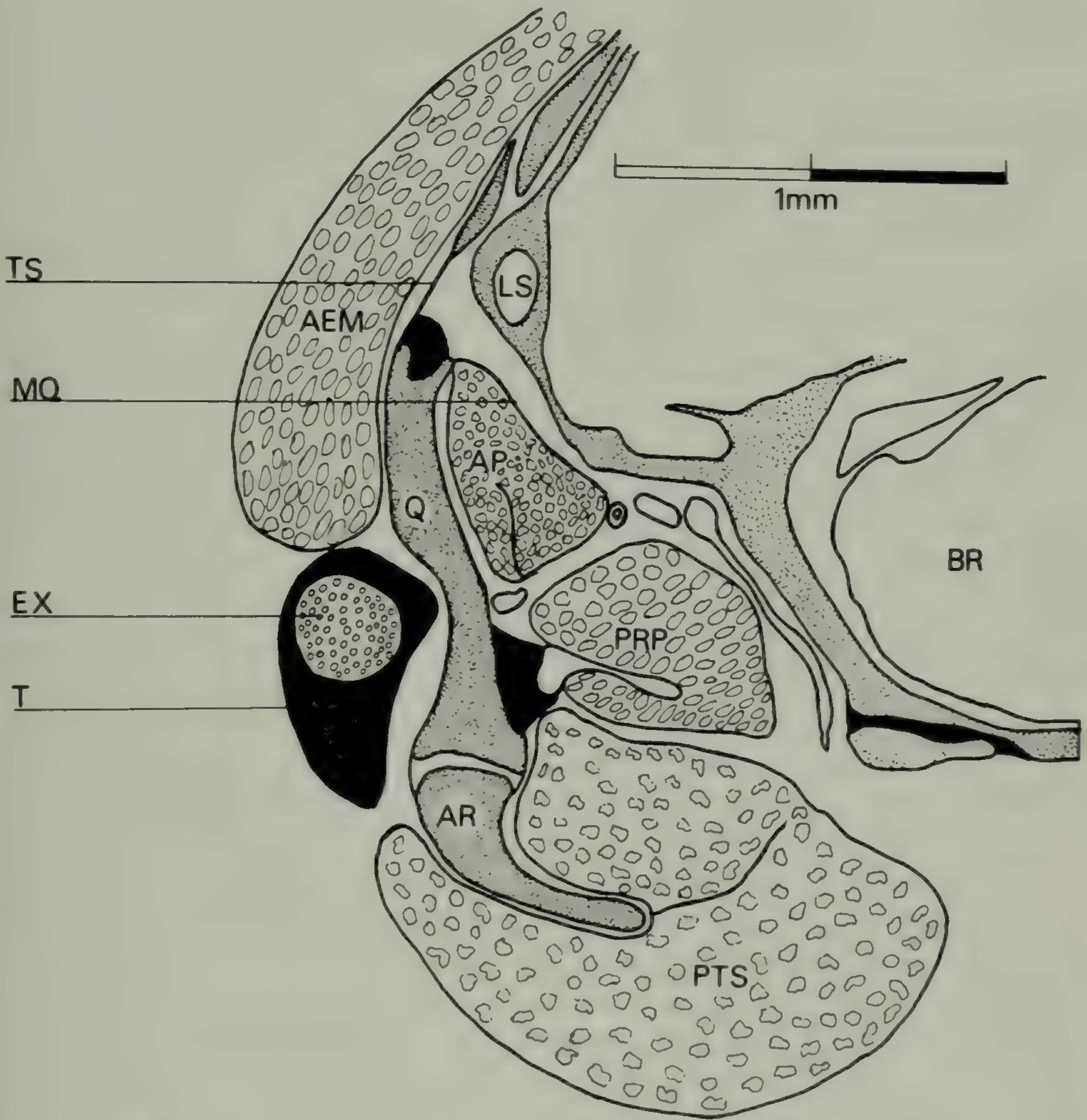

Fig. 13. Cross-section of the skull at the level of the quadrate.

insertion of the fibres arising in line with the jaw articulation on the medial surface of the quadrate. This tendon extends anteriorly for a short distance to attach immediately anterior to the articular facet on the dorsomedial surface of the articular process. The rest of the fibres straddle the mandible and insert dorsomedially on the surangular, within and around the adductor fossa (Fig. 11) on that part of the prearticular forming the ventral rim of the adductor fossa, and anterior to the fossa on the dorsomedial surface of the prearticular. A few fibres attach dorsomedially to the posterior process of the coronoid. In addition, fibres of this part of the muscle also insert on a small, vertical tendon running dorsally along the surangular ridge and situated within the muscle itself (Fig. 11). The tendon extends from the anterior border of the muscle to a point in line with the anterior border of the mandibular ramus of V, and fibres insert along its lateral and medial surfaces. The lateral fibres of the muscle insert on the mandibular shelf (Fig. 11), attaching dorsolaterally on to the surangular and dentary from the articular facet to near the base of the coronoid process.

A posterolateral branch of the mandibular ramus of V ramifies within the medius portion of the external adductor, with one branch piercing the medial lamina of the quadrate tendon to innervate the posterior adductor.

Musculus adductor mandibulae internus

According to Lakjer (1926) the third main division of the adductor mandibulae group, the internal adductor musculature, consists of two separate muscles, the m. pseudotemporalis and m. pterygoideus. Both muscles are present in *Typhlosaurus aurantiacus* as well-defined groups of fibres situated at right angles to one another.

The musculus adductor mandibulae internus pseudotemporalis (p, Figs 9–11) is a single, dorsoventral group of fibres located anteriorly within the temporal indentation, and although the bulk of its fibres are concentrated dorsomedially to the coronoid process, the muscle extends posteriorly to the anterior border of the mandibular ramus of V. As required by the classical definition it is situated medially to the maxillary, laterally to the ophthalmic and anteriorly to the mandibular rami of V. It lies medially to and against the superficial, anteromedially to the medius and anteriorly to the profundus portions of the external adductors; anteromedially to the posterior adductor muscle; laterally to the levator pterygoideus muscle and the epipterygoid bone, and anterolaterally to the pterygoideus muscle.

It arises fleshily from the anterolateral surfaces of the parietal downgrowth and the anterior superior process of the pro-otic, anterior to the origin of the profundus portion of the external adductor as well as from the lateral surface of the pro-otic membrane and the dorsal part of the epipterygoid bone.

The muscle inserts on the medial surface of the coronoid bone, utilizing the medial coronoid groove which extends from the apex of the coronoid process to the medial surface of the posterior process of the coronoid bone (Fig. 10). A small tendon attaching to the coronoid bone extends along the lower rim of the medial coronoid groove and underlies the pseudotemporalis muscle, receiving the insertion of its medial fibres (Fig. 9). Behind the coronoid bone a few fibres insert on to the medial surface of the prearticular bone (Fig. 11).

The muscle is innervated by a branch of the mandibular ramus of V which leaves the anterior border of the ramus directly below the Gasserian ganglion and courses anteriorly for a short distance to enter the muscle posterodorsally.

The musculus adductor mandibulae internus pterygoideus (pts), is the largest single muscle in the head of *Typhlosaurus aurantiacus* and extends from the infra-orbital fenestra to the posterior extremity of the mandible. It has a small head which expands posteriorly to form a large rounded masticatory cushion, appropriately termed 'Kauwulst' by Lakjer (1926). The 'Kauwulst' is the most prominent part of the muscle and, with its opposite number, limits the aperture of the throat. It lies deep to the intermandibularis posterior muscle and the mandibulo-hyoid musculature, medially to the insertional tendon of the cervicomandibularis muscle and laterally to the protractor pterygoidei muscle and the pterygoid bone.

The muscle arises mainly from the outer surface of the pterygoid bone (Fig. 9) and from the inner surface of an extensive tendon originating lateral to the infra-orbital fenestra. Anteriorly the muscle is divided into two short slips, one arising dorsally from both the posterolateral surface of the palatine and the anterolateral border of the pterygoid and the second one arising ventrally on the posterolateral border of the palatine and the anterolateral surface of the pterygoid. The two muscle slips become confluent at a point in line with the anterior border of the levator pterygoideus muscle.

Some fibres arise fleshily along the outer lateral and ventral surface of the gutter-shaped pterygoid bone (Fig. 11). The major part of the origin, however, is from the exceptionally strong tendon arising lateral to the infra-orbital fenestra on the ventral surface of the palatal complex. The tendon arises behind the ventrolateral process of the maxillary on the ventral surface of the ectopterygoid, the posteroventral surface of the palatine and on the ventral surface of the pterygoid in front of the basipterygoid recess. Anteriorly the tendon covers the origin of the ventral slip of muscle and forms a thick pad medial to the angle of the mouth (Fig. 9). The pad presumably protects the fibres from damage by deflecting the coronoid process laterally during adduction of the jaw. Posteriorly the tendon broadens to cover the anterior two-thirds of the ventral surface of the muscle. Most of the fibres of the pterygoideus muscle arise from the inner surface of this tendon.

The muscle inserts on the retroarticular process of the mandible (Fig. 13). In front of the process the ventral border of the mandible is concave to accommodate the lateral fibres of the muscle which wrap around the jaw behind the posteroventral extremity of the dentary. The muscle envelops the retroarticular process, with fibres inserting on to its medial, ventral and lateral surfaces. Medial to the jaw a ribbon-like tendon lies within the muscle and attaches ventrally to the retro-articular process (Fig. 13). Its dorsal and ventral surfaces are utilized for insertion.

The muscle is innervated by a branch of V which leaves the mandibular ramus medially, in line with the posterior supra-angular foramen, to pierce the muscle laterally.

Intermandibular musculature

The intermandibular muscles, innervated by V, form part of the trigeminal musculature. Situated anteroventrally to the constrictor colli, their fibres extend transversely between the rami of the lower jaws as thin superficial sheets of muscle, deep only to the skin and to the insertional tendon of the cervico-mandibularis muscle. Two portions, an anterior and a posterior, are present.

The m. intermandibularis anterior (ia, Figs 9–10), four to six fibres in thickness, lies anteriorly between the rami of the lower jaws. It is laterally interrupted at right angles by bundles of the geniohyoideus muscle which insert anteroventrally on the jaw. According to Camp (1923) these interdigitations (of which there are five in *Typhlosaurus aurantiacus*) are always present in lizards. The muscle lies superficially to the geniohyoideus and genioglossus muscles and can be divided into a more posteriorly lying superficial portion and a more anteriorly lying profundus portion.

The superficial portion arises medially on the jaw (Fig. 10) between the posterior mylohyoid foramen and the combined foramen for the anterior mylohyoid and the infra-alveolar nerves, along the medial surface of the pre-articular, splenial and dentary bones. It inserts anteriorly along the ventral midline onto the sheet of fascia receiving the insertion of the constrictor colli muscle. Three bundles of geniohyoideus fibres interdigitate with the superficial portion of the intermandibularis anterior muscle.

The profundus portion of the m. intermandibularis anterior lies immediately anterior to the superficial portion, posteriorly overlain by the latter. It arises medially to the jaw from the dorsolateral surface of the sublingual gland and the outer surface of the buccal lining, dorsal to the gland. The origin extends from a point in line with the anterior mylohyoid and the infra-alveolar foramen to just behind the jaw symphysis. The muscle inserts tendinously in the ventral midline anterior to the superficial portion of the intermandibularis anterior muscle. Two bundles of the geniohyoideus fibres interdigitate with the profundus portion.

The intermandibularis anterior is innervated by a branch of the posterior mylohyoid nerve, which enters the superficial portion posteriorly, and by a branch of the anterior mylohyoid nerve, which enters the profundus portion superficially.

The m. intermandibularis posterior (ip, Fig. 12), two fibres in thickness, lies immediately behind the intermandibularis anterior. The two muscles are separated by the most posterior interdigitation between the geniohyoideus and intermandibularis anterior muscles. The intermandibularis posterior does not interdigitate with the geniohyoideus muscle and is well separated from the constrictor colli. It covers the throat ventrally, lateral to the midline, and lies superficially to the hyoglossus, the genioglossus and the geniohyoideus muscles, the masticatory cushion (Kauwulst) of the pterygoideus muscle and the hypoglossal nerve (Fig. 12).

The m. intermandibularis posterior arises tendinously from a thin sheet of fascia which covers the pterygoideus muscle laterally (Fig. 12) and attaches to the lateral surfaces of the surangular and dentary bones between the jaw articulation and the posterior mylohyoid foramen. The muscle inserts tendinously in the ventral midline on to the same sheet of fascia which receives the insertion of the constrictor colli muscle and the intermandibularis anterior muscle (Fig. 12).

It is innervated by a branch of the posterior mylohyoid nerve, entering the muscle superficially via the posterior mylohyoid foramen.

Tongue musculature

In *Typhlosaurus aurantiacus* the tongue is of the usual scincid type, bluntly triangular with a bifurcate apex and posteriorly divided into two roots situated lateral to the glottis. Behind the apex its dorsal surface is covered with scale-like papillae, on which glandular surfaces are restricted to the basal portions. According to Camp (1923) the position of the glandular surfaces is a diagnostic feature of the Scincomorpha.

The tongue is composed of fibres of both extrinsic and intrinsic musculature. The intrinsic fibres control the shape of the tongue, while motion is controlled by the extrinsic fibres. Sondhi (1958) found that in some Indian reptiles the apparently distinct groups of intrinsic fibres are actually parts of the hyoglossus muscle and do not deserve independent status. In *Typhlosaurus aurantiacus* these fibre groups are equally distinct and in view of the marked differences between their orientation and that of the hyoglossus muscle, they will be described separately.

Extrinsic muscles

The m. hyoglossus (hg, Figs 9–12) is a paired longitudinal muscle, extending parallel to the midline from the hyoid apparatus to the anterior tip of the tongue. Posteriorly the muscle is dorsoventrally flattened and lies ventrolaterally to the trachea and the oesophagus, laterally to the first ceratobranchial and dorsolaterally to the posterior part of the geniohyoideus muscle. Anteriorly it becomes cylindrical, turning dorsally to the undersurface of the tongue to lie laterally to the lingual process of the hyoid, medially to the geniohyoideus muscle, and ventrolaterally to the glottis. It is sheathed by fibres of the vertical intrinsic musculature. The most anterior part of the muscle lies dorsomedially to the genioglossus muscle, and tapers towards the jaw symphysis to terminate ventrally to the anterior tip of the tongue.

The muscle arises superficially in the throat region from the anterior surface of the first ceratobranchial, medially to the origin of the geniohyoideus lateralis muscle, ventrolaterally to the oesophagus and dorsolaterally to the origin of the geniohyoideus medialis muscle. It inserts fleshily along the ventral surface of the tongue, between the medial and lateral vertical fibres of the intrinsic musculature and medially to the insertion of the genioglossus muscle. The muscle is innervated by a branch of the hypoglossal nerve.

The m. genioglossus (ggl, Figs 9–12) is a paired muscle, lying laterally to the ventral midline and extending from the jaw symphysis to the posterior border of the tongue. In front it lies dorsolaterally to the geniohyoideus medialis muscle, ventrolaterally to the hyoglossus muscle, and medially to the sublingual gland. At the back the muscle extends laterally around the ventral surface of the sublingual gland and behind it the fibres lie ventrally to the lateral margin of the oral membrane. A small cylindrical group of fibres separates anteroventrally from the genioglossus muscle and extends posteriorly, lying ventromedially to the genioglossus muscle and dorsally to the geniohyoideus medialis muscle. In line with the glottis the fibres of this bundle become confluent with those of the geniohyoideus medialis muscle. It is innervated by a minute ramus branching from the hypoglossal nerve.

The genioglossus arises tendinously at the jaw symphysis, taking origin from the inner ventral surface of the dentary immediately lateral to the symphysis, from the connective tissue surrounding the symphysis and, in the midline, from the sheet of fascia covering the throat musculature ventrally. It inserts along the ventral surface of the tongue, laterally to the hyoglossus muscle and the lateral group of vertical intrinsic fibres, and interlaces with the transverse fibres of the intrinsic musculature. The muscle is innervated by a branch of the hypoglossal nerve.

Intrinsic musculature

The intrinsic muscles are innervated by the hypoglossal nerve and consist of three groups of fibres, i.e. the vertical lingual, the longitudinal lingual and the transverse lingual fibres, and although they interweave to some extent each group remains distinct.

The m. verticalis linguae (vl, Figs 9–11) consists of a superior and an inferior group of fibres. The superior fibres lie dorsally to the transverse lingual muscle and form the papillae of the tongue. The inferior fibres lie ventrally to the transverse lingual muscle, interlace with its fibres, and extend from the apex of the tongue to the glottis. These fibres consist of a medial and a lateral group. The lateral group lies between the genioglossus and the hyoglossus muscles while the medial group lies between the hyoglossus muscle and the midline. The two groups meet tendinously ventral to the hyoglossus muscle.

The m. transversalis linguae (tl, Figs 9–11) lies between the inferior and superior vertical fibres. Its fibres extend across the width of the tongue from the apex to the roots and interlace with the fibres of the inferior vertical, the hyoglossus and the genioglossus muscles.

The m. longitudinalis linguae (ll, Figs 9–10) lies ventrally along the rim of the tongue, laterally to the insertion of the genioglossus muscle on either side. It extends from behind the apex of the tongue to nearly in line with the glottis as a single cylindrical bundle of fibres, breaking up into smaller bundles posteriorly and becoming obscured by the insertion of the genioglossus muscle.

The m. geniohyoideus lateralis (ghl, Fig. 12) is a narrow muscle extending between the ventral surface of the jaw and the hyoid apparatus. It lies ventromedially to the jaw, ventrolaterally to the genioglossus muscle, deep to the intermandibularis posterior muscle, and ventrally to the 'Kauwulst' of the pterygoideus muscle.

It arises fleshily on the ventral surface of the jaw from a short distance behind the symphysis to the posterior mylohyoid foramen. The origin consists of five successive bundles of longitudinal fibres interlacing with the fibres of the intermandibularis anterior muscle. The muscle inserts on the anterolateral tip of the sole remaining posterior prong of the hyoid apparatus (usually taken to be the first ceratobranchial). The insertion is fleshy and lies lateral to that of the geniohyoideus medialis and hyoglossus muscles. The muscle is innervated by a branch of the glossopharyngeal nerve.

The m. geniohyoideus medialis (ghm, Figs 9–12) is a superficial group of fibres extending from the anteroventral surface of the genioglossus muscle to the hyoid apparatus. The muscle lies laterally to the ventral midline, deep to the intermandibularis musculature, ventromedially to the genioglossus muscle and below the bundle of fibres extending between it and the genioglossus muscle. Posteriorly the muscle is flattened dorsoventrally and lies ventromedially to the hyoglossus muscle, deep to the intermandibularis posterior muscle and medially to the hypoglossal nerve. Anteriorly the muscle becomes triangular in cross section and lies deep to the intermandibularis anterior muscle.

The muscle arises tendinously behind the origin of the genioglossus muscle, from the deep surface of the sheet of fascia covering the throat musculature ventrally and inserts fleshily along the ventral surface of the first ceratobranchial, ventromedially to the origin of the hyoglossus muscle. The muscle is innervated by a branch of the glossopharyngeal nerve.

Depressor mandibulae group

The m. depressor mandibulae (Figs 14–16) is a superficial sheet of fibres behind the adductor musculature. It lies laterally to the stapedial artery, the lateral head vein and the hyomandibular ramus of VII. On its ventrolateral surface it is obliquely overlain by the prominent cervicomandibularis muscle which in its turn is covered by the dorsoventral fibres of the sheet-like constrictor colli muscle. There is no indication in either *Typhlosaurus aurantiacus* or *Acontias meleagris* that the depressor mandibulae and cervicomandibularis muscles are continuous.

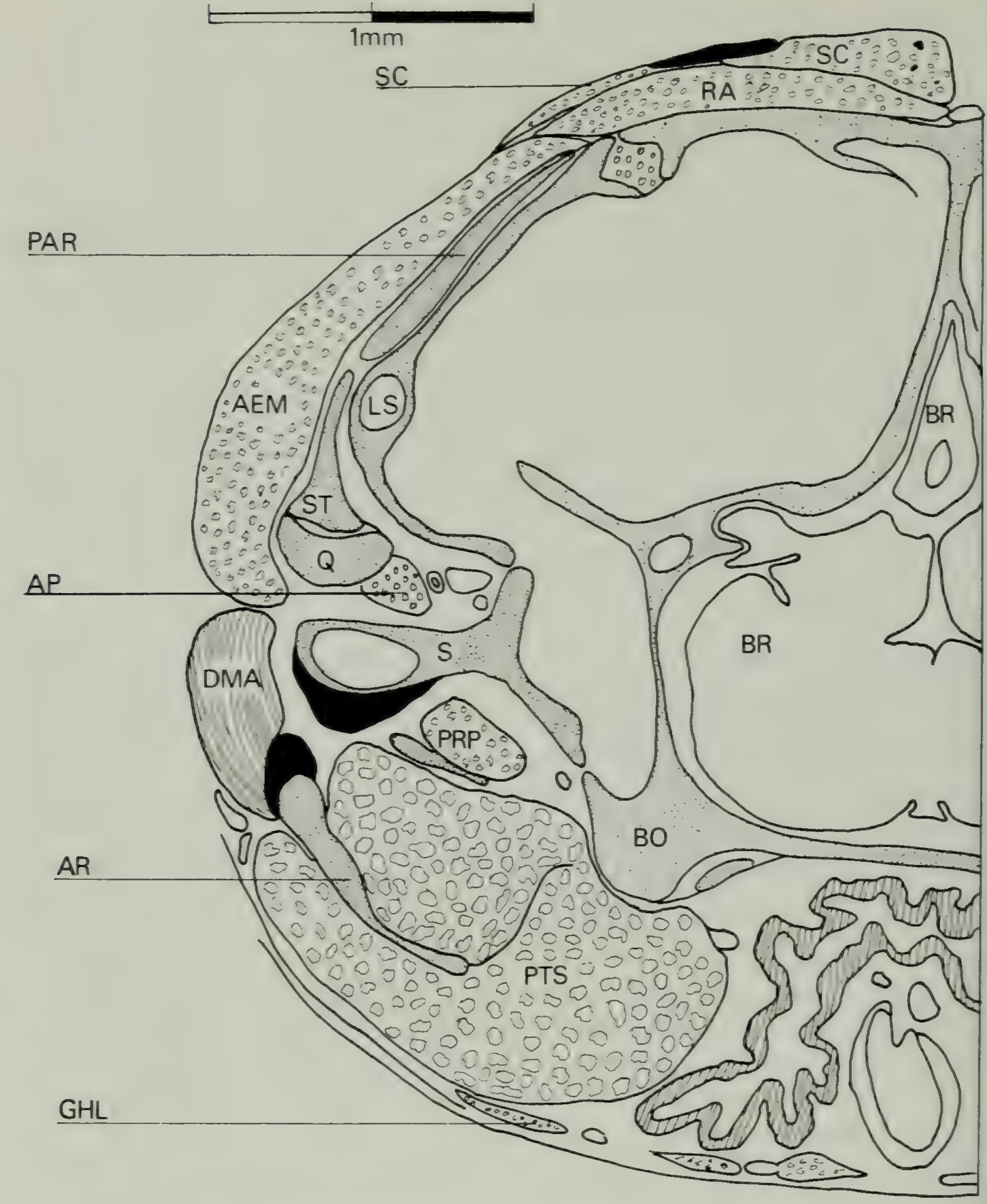

Fig. 14. Cross-section of the skull at the level of the stapes.

The depressor mandibulae consists of an anterior portion arising cranially and a posterior portion arising cervically. The anterior portion (dma, Figs 7, 14–15) is spindle-shaped and lies immediately behind the stapes. It arises fleshily from the anterolateral surface of the fused exoccipital-opisthotic bone, posterodorsally to the quadrate head, and extends vertically downwards, laterally to the posterior half of the stapedial footplate, to insert fleshily on the dorsal

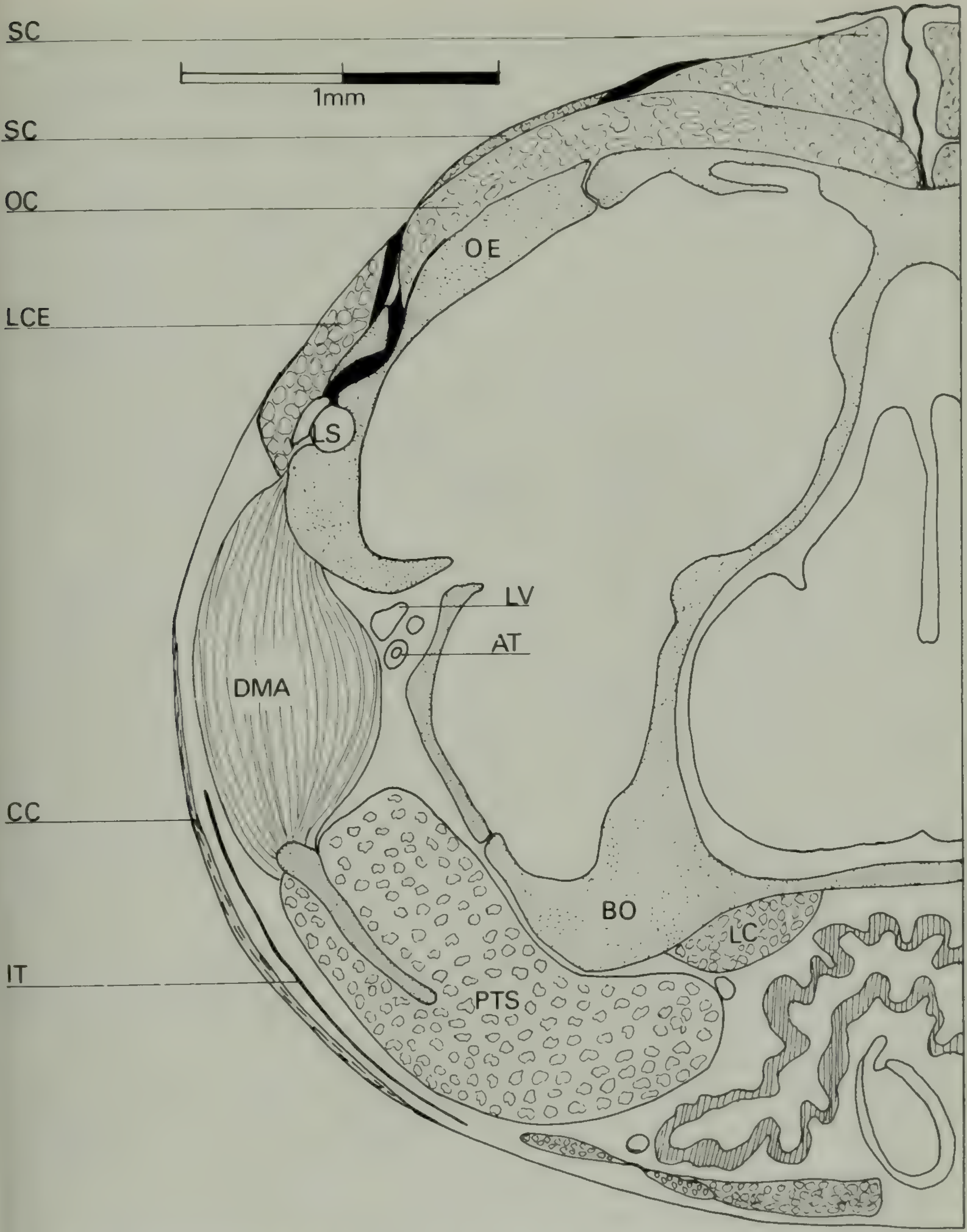

Fig. 15. Cross-section of the skull at the level of the anterior portion of the depressor mandibulae.

surface of the retro-articular process behind the tendon connecting the stapes to the mandible.

The posterior portion (dmp, Fig. 16), a thin triangular sheet of fibres lateral to the obliquus capitis magnus muscle and the innervations of the longissimus and episternocleidomastoideus muscles, lies against the posterior border of the cranial portion of the depressor mandibulae. It arises along the insertional tendon of the longissimus cervicis muscle, ventrolateral to the spinalis capitis

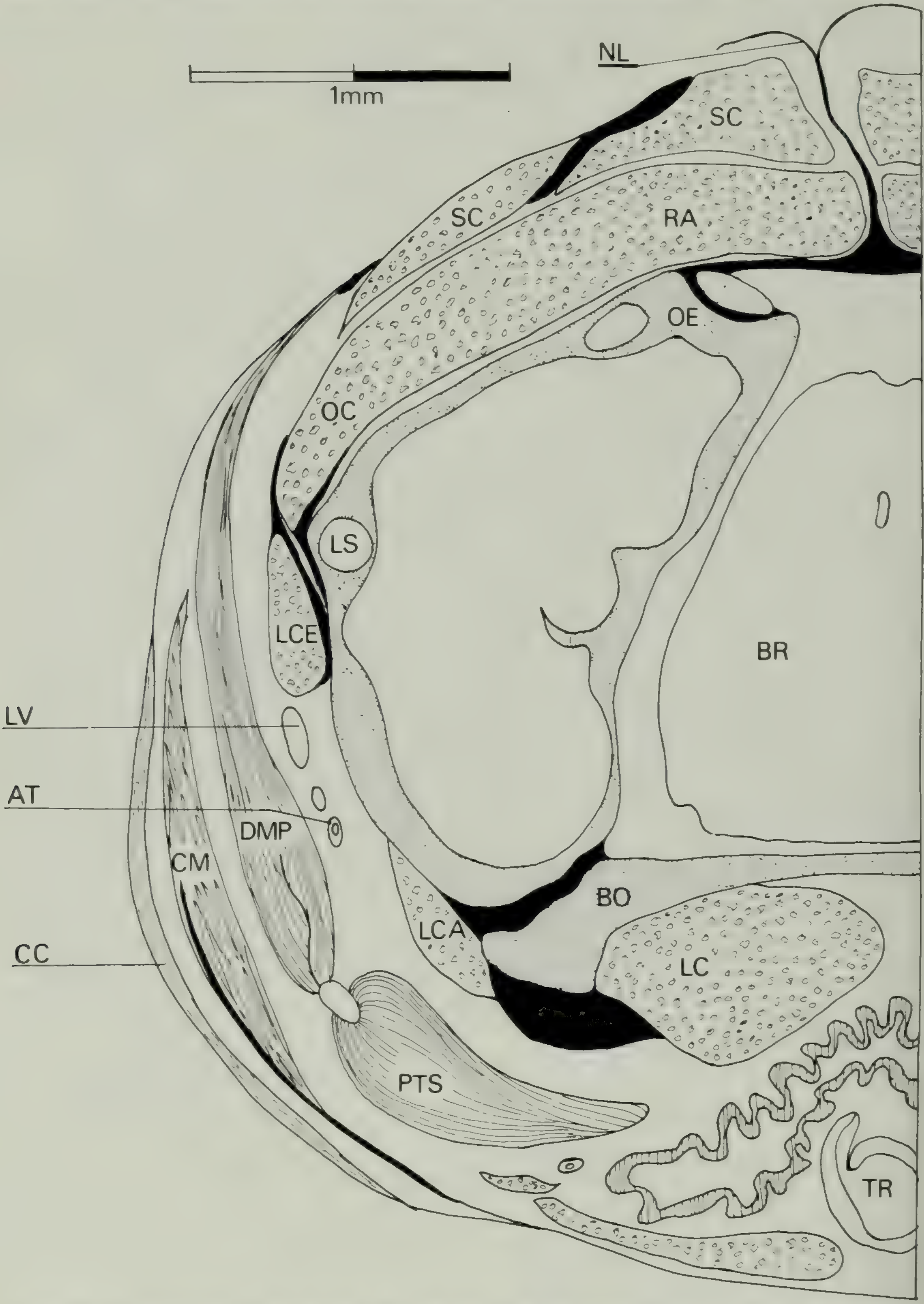

Fig. 16. Cross-section of the skull at the level of the posterior portion of the depressor mandibulae.

muscle and between the origin of the cervicomandibularis muscle and the posterodorsal border of the adductor mandibulae musculature. The fibres converge anteroventrally to insert behind those of the cranial portion by means of a small tendon on to the posterodorsal extremity of the retro-articular process of the mandible.

The depressor mandibulae is innervated by the hyoid ramus of VII, which branches off behind the stapedial footplate from the hyomandibular ramus, pierces the medial surface of the muscle and courses anteriorly for a short distance within it.

The m. cervicomandibularis (cm, Figs 6–7, 16) is a large elongated sheet of fibres medial to the constrictor colli muscle. It extends antero-ventrally, superficial to the cervical musculature, from the level of the seventh dorsal vertebra to the anteroventral surface of the jaw. It lies lateral to the episternocleidomastoideus muscle, the longissimus cervicis and capitis muscles, and the anterior parts of the iliocostalis system and the oblique hypaxial muscles.

The muscle arises fleshily from the anterolateral surface of the iliocostalis system and the oblique hypaxial muscles, from the longissimus cervicis muscle, and along its border from the dorsal intermuscular septum. Its fibres extend forward only as far as the posterolateral surface of the 'Kauwulst' of the pterygoideus muscle where they attach to a thin sheet of fascia which covers the 'Kauwulst' laterally and ventrally and lies superficial to the throat muscles. Anteriorly the tendon becomes aponeurotic and inserts along the ventral surface of the jaw, from the anterior border of the posterior intermandibular muscle to just lateral to the symphysis.

The m. cervicomandibularis is innervated by a branch of VII which pierces the medial surface of the muscle in line with the occipital condyle of the skull.

The m. constrictor colli (cc, Figs 5, 15–16) is a thin superficial sheet of fibres covering the cervical region immediately below the skin. Its fibres extend anteroventrally from the cervical region to cover the pterygoideus muscle posterolaterally and the cervicomandibularis muscle anteroventrally. The muscle is triangular in lateral aspect and its anterior border lies immediately behind the extracolumella. The upper border of the muscle tapers posteroventrally and it terminates at a point ventrolateral to and approximately in line with the third vertebra.

The muscle arises fleshily from a thin superficial sheet of cervical fascia extending ventrally from the dorsal intermuscular septum, situated between the transversospinalis and longissimus systems, to insert ventrolaterally in the cervical region on to a superficial sheet of fascia covering the throat from the jaw symphysis posteriorly to the rectus abdominis muscles.

The muscle is innervated by a branch of the hyomandibular ramus of VII which passes through the cervicomandibularis muscle to enter the deep surface of the constrictor colli in line with the posterior border of the condyle of the skull.

Cervical musculature

In contrast to non-fossorial lizards, the cervical extensor and flexor muscles in *Typhlosaurus aurantiacus* play an active role during locomotion and especially during burrowing movements. However, in spite of this added function the distribution of the individual muscles retains a pattern common to saurians in general.

The nuchal ligament is a vertical mid-dorsal sheet in the cervical region extending from the occiput to the neural spine of the axis. Dorsally the ligament is continuous with the fascia covering the transversospinalis system. This fascia is laterally continuous with the dorsal intermuscular septum lying between the transversosponalis and longissimus systems.

The m. spinalis capitis (sc, Figs 6, 12, 14–16) is a flat, dorsally situated muscle extending immediately below the skin from the level of the twelfth vertebra to the occiput. It lies lateral to the nuchal ligament and dorso-medial to the anterior part of the longissimus dorsi muscle and its cervical derivative, the longissimus cervicis. The muscle covers the rectus capitis anterior and obliquus capitis magnus muscles. The lateral fibres arise fleshily from the lateral margin of the dorsal intermuscular system.

The fibres insert tendinously on to the posterodorsal surface of the parietal bone. The insertion is confined to a shallow depression on the parietal anterior to the supra-occipital-parietal suture and lateral to the small mid-dorsal ridge formed by the ascending process of the tectum synoticum.

The muscle is innervated by a branch of the dorsal ramus of the first spinal nerve which passes between the rectus capitis posterior and the obliquus capitis magnus muscles.

The m. rectus capitis poşterior and the m. obliquus capitis magnus are partially fused and appear as a single group of fibres. However, in the interests of clarity they will be described separately.

The m. rectus capitis posterior (rp, Figs 6, 8) extends from the atlas to the occiput. It lies ventral to the spinalis capitis muscle, lateral to the nuchal ligament, dorso-medial to the longissimus cervicis muscle and antero-medial to the obliquus capitis magnus muscle, which arises posterior to it. In *Typhlosaurus aurantiacus* the rectus capitis posterior is a single muscle and it probably represents the fused rectus capitis superficialis and profundus muscles still present, although partially fused, in such forms as *Iguana iguana* (Olson 1936). The rectus capitis posterior muscle can be distinguished from the obliquus capitis magnus muscle by the passage of the dorsal ramus of the first spinal nerve between them as in *Ctenosaura pectinata* (Oelrich 1956).

The muscle arises fleshily from the lateral surface of the axial neural arch and the aponeurotic fascia covering the atlanto-occipital gap. Some fibres also arise from the dorsal surface of the obliquus capitis magnus muscle.

The fibres insert fleshily, deep to the spinalis capitis muscle and dorso-medial to the insertion of the obliquus capitis magnus muscle, on to the dorsal surface of the supraoccipital bone and that part of the fused exoccipital-opisthotic bone dorsal to the ridge formed by the lateral semicircular canal of the internal ear.

The muscle is innervated by a branch of the dorsal ramus of the first spinal nerve.

The m. obliquus capitis magnus (oc, Figs 6, 8) extends from the fifth vertebra to the lateral margin of the fused exoccipital-opisthotic bone. It lies ventral to the spinalis capitis muscle, posterolateral to the rectus capitis posterior muscle, dorsal to the anterior part of the spinalis dorsi muscle, dorsal to the rectus capitis anterior muscle and medial to the longissimus cervicus muscle.

It arises fleshily from the dorsal extremities of the neural spines of the third, fourth and fifth vertebrae, the tendinous tissue connecting the spines and from the fascia covering the spinalis dorsi muscle.

The fibres extend obliquely forward and insert tendinously on to the lateral margin of the fused exoccipital-opisthotic bone, attaching to the ridge formed by the lateral semicircular canal of the internal ear, ventrolateral to the rectus capitis posterior muscle and dorsomedial to the insertion of the longissimus cervicis muscle.

The muscle is innervated by the dorsal ramus of the first spinal nerve.

The m. longissimus dorsi lies ventrolateral to the transversospinalis system and dorsal to the heads of the ribs. At the level of the fourth vertebra it divides into a dorsal and a ventral group of fibres. The dorsal group, the m. longissimus cervicis (lce, Figs 6–8) lies ventrolateral to the spinalis capitis and rectus capitis posterior muscles and lateral to the obliquus capitis magnus muscle. The muscle arises fleshily approximately from the level of the seventh to the second vertebrae from the fibres of the longissimus dorsi muscle. It extends anteriorly dorsal to the longissimus capitis muscle and lateral to the obliquus capitis magnus muscle, to insert tendinously on to the lateral margin of the fused exoccipital-opisthotic bone, lateral to the insertion of the obliquus capitis magnus muscle and medial to the insertion of the episternocleidmastoideus muscle.

The muscle is innervated by the dorsal ramus of the first spinal nerve.

The ventral group of fibres, the m. longissimus capitis (lca, Fig. 8), extends anteroventrally from the level of the fourth vertebra to the basal tuberosity of the basi-occipital bone. It lies ventral to the longissimus cervicus muscle, medial to the episternocleidomastoideus muscle, dorsolateral to the longus colli muscle and lateral to the rectus capitis anterior muscle. The fibres arise fleshily from the longissimus dorsi muscle and the synapophysis of the first four vertebrae to insert tendinously on to the basal tuberosity lateral to insertion of the rectus capitis anterior muscle and dorsomedial to the insertion of the longus colli muscle.

The muscle is innervated by a branch of the dorsal ramus of the first spinal nerve.

The m. rectus capitis anterior (ra, Fig. 8) is a group of short fibres extending from the axis to the occiput. The muscle lies ventrolateral to the axis, the atlas and the occipital condyle of the skull; medial to the longissimus capitis muscle and dorsal to the anterior part of the longus colli muscle with which some of its ventral fibres are confluent.

It arises fleshily on the ventrolateral surface of the axis medial to the synapophysis and ventrolaterally on the atlas. The fibres insert fleshily on to the basioccipital and exoccipital-opisthotic bones. The insertion lies ventral to the insertion of the rectus capitis posterior muscle, dorsal to the insertion of the longus colli muscle and dorsomedial to the insertion of the longissimus capitis muscle.

The muscle is innervated by a branch of the first spinal nerve.

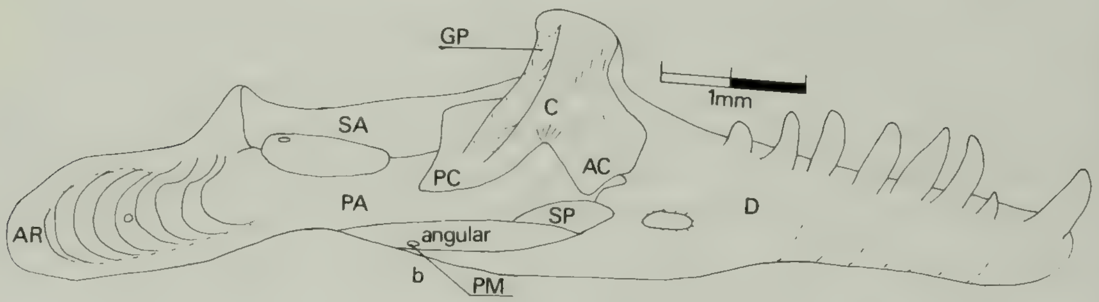

Fig. 17. Camera lucida drawing of the left lower jaw; lingual view.

DISCUSSION AND CONCLUSIONS

General

The morphology of fossorial skinks in general is paralleled by that of snakes in many ways and it is therefore interesting to note that according to the theory of Walls (1942) snakes originated as fossorial forms. Any evaluation of the musculature of *Typhlosaurus aurantiacus* must be made in the light of the fact that the animal leads a predominantly subterranean existence which does not involve the construction of burrows. Huey *et al.* (1974) describes *Typhlosaurus* as a sand swimming lizard which normally moves in a lateral sinuous path beneath the sand. *T. aurantiacus* has a subterminal mouth as in other fossorial lizards, e.g. *Acontias*. The position of the mouth prevents soil particles from entering the buccal cavity during burrowing movements. De Weerdt (1971) indicates that it is important to a fossorial lizard like *Dibamus* to use its mouth in a terminal position. This argument is based on the assumption that the lizard lives in a burrow and encounters its prey directly in front of it. Neither *Typhlosaurus* nor probably *Dibamus* lives in a burrow and consequently prey may be approached from any angle.

The animal uses its head as a burrowing tool, and the skull and its associated musculature are consequently strongly modified. Temporal arches and posttemporal fenestrae are absent. The elongated temporal region is strengthened by the lateral downgrowth of the parietal and the broad anterior superior processes of the pro-otic. These structures also serve as areas of origin to the adductor musculature. The occipital region is strengthened by the fused exoccipital and ophisthotic bones and the expanded nature of the occiput allows the cervical musculature to insert relatively far forward on to the skull.

As in *Dibamus* (Gasc 1968) *Typhlosaurus aurantiacus* lacks a m. levator bulbi. This condition is probably associated with the degeneration of the eyes. According to Haas (1973) the structural diversity of the m. levator bulbi in lizards appears not to be controlled by phylogenetic factors but rather by functional factors such as the presence or absence of a movable lower eyelid or a general reduction of the visual apparatus.

The m. pseudotemporalis is single in *Typhlosaurus aurantiacus* as in the Gekkonidae, the Pygopodidae and the snakes. De Weerdt (1971) describes a single m. pseudotemporalis in *Dibamus* but fails to define the position of the muscle in relation to the maxillary ramus of V. It may well be that the muscle is in fact part of the m. adductor mandibularis externus. Gasc (1968) describes a m. pseudotemporalis in *Dibamus* consisting of two parts. Haas (1973) interprets Gasc's description as pertaining only to the posterior of the two portions. However, Gasc, on page 135, clearly states that: 'Une nappe profonde (fig. 9) formée par deux chefs. . . . Cette nappe pourrait correspondre, d'après ses insertions, aux deux chefs du m. adductor mandibularis medius (= pseudotemporalis); toutefois, la branche maxillaire du trijumeau passe ici au-dessous de ce plan musculaire.' From Gasc's figure 9 it is clear that the maxillary ramus of V lies medial to the m. pseudotemporalis. It is probable therefore that this muscle forms part of the m. adductor mandibularis externus and not the m. adductor mandibularis internus. According to Haas (1973) the gekkonids and pygopodids lack the m. pseudotemporalis superficialis but retain the profundus portion of the muscle which consists of an anterior and a posterior part. It is probable that the single muscle retained in *T. aurantiacus* represents the profundus portion of the m. pseudotemporalis and that the reduction of the m. pseudotemporalis in this animal is related to the loss of the temporal arches as Haas (1973) believes it to be in the case of gekkonids, pygopodids and snakes.

The depressor mandibulae is a relatively small muscle and (in theory) its position close to the fulcrum of the jaw is not functionally optimal. Since the opening of the jaw is usually assisted by gravity this condition is not a liability. However, in a lizard which feeds subterraneously the surrounding pressure of the soil may demand a more sophisticated arrangement of the jaw opening muscles. In *Typhlosaurus aurantiacus* the cervicomandibularis is probably the main jaw opening muscle since its origin on the neck musculature and ventral insertion on the jaw makes it ideally suited for this purpose. Camp (1923) notes that the cervicomandibularis muscle is enormously developed in all burrowers.

From the forwardly extended insertion of the cervical musculature on to the occiput and the lateral extension of the synapophyses of the axis and the three following vertebrae it is evident that this group of muscles plays an important role in locomotion. It serves to flex and extend the skull as well as stiffen the atlanto-occipital joint during burrowing. The degree of fusion between individual cervical muscles seems logical in the light of their function.

Cranial kinesis

Versluys (1910, 1912) described the movable joints of the reptilian skull. He divided the skull into an 'occipital segment' consisting of the bones of the braincase and the parasphenoid, and a 'maxillary segment' comprising the rest of the skull. The intracranial movements between the two segments are known as kinesis and were interpreted by Versluys as a mechanism for increasing the gape of the mouth by lifting the snout. Various degrees of kineticism exist, and skulls ranging from akinetic, with little or no movement between the 'segments', to amphikinetic, in which more than two movable parts are found. The constrictor dorsalis group of muscles is responsible for the kinetic movements of the skull.

Versluys based his conclusions on morphological studies, but recent workers have made use of sophisticated methods to study live material. Frazetta (1962) who revised Versluys's terminology, used motion pictures to record the capture of prey as well as electrical stimulation and biomechanical analysis of the muscles. Iordansky (1970) used biomechanical analysis to extend the approach of Frazetta. In contrast to Versluys, Frazetta concluded that kinesis actually lessens oral gape. However, in spite of the advanced techniques employed by them, Frazetta and Iordansky are not in full agreement on certain aspects of kinesis.

It is evident that kinesis is a complex mechanism of which the functional significance is not yet fully explained. This is also clear from the variable nature of the constrictor dorsalis group of muscles in a form such as *Sphenodon*. Frazetta (1962) describes *Sphenodon* as akinetic whereas Ostrom (1962) describes a specimen which has both a levator pterygoidei and a protractor pterygoidei muscle. According to Ostrom, in previously described specimens of *Sphenodon* either one of these muscles were present but never both. The study of cranial kinesis therefore requires the application of sophisticated techniques to live specimens as well as the dissections of numerous examples of the same species. The scope of this paper and the paucity of material precludes an in-depth study of cranial kinesis in *Typhlosaurus aurantiacus* but, since the cranial muscles have been described in detail, a brief summary will be given here.

According to Bellairs (1969) fossorial lizards tend to become monokinetic or even akinetic. A reduction of intracranial movements seems logical in the light of strengthening the skull for burrowing. Usually it appears that the metakinetic bending plane between the supraoccipital and parietal bones is reduced in favour of the mesokinetic bending plane between the parietal and frontal bones as in *Acontias* (De Villiers 1939, Brock 1941, Van der Merwe 1944); *Monopeltis capensis* (Kritzinger 1946); *Anniella* (Toerien 1950, Bellairs 1969); *Nessia* (Bellairs 1969) and *Dibamus* (De Weerdt 1971). According to Leonard (1973) the less specialized burrowing skink *Scelotes* is amphikinetic.

In *Typhlosaurus* the presence of a small levator pterygoidei muscle, a substantial protractor pterygoidei muscle, a synovial articulation between the quadrate and the skull and a movable basipterygoid articulation clearly indicate a certain amount of intracranial movement. Because of the posterior expansion of the skull, the occipital bones have become fused and the insertional areas of the cervical musculature have increased to such an extent that the spinalis capitis muscle inserts dorsally on the posterior part of the parietal, anterior to the position of the metakinetic bending plane.

The position of this muscle suggests a sharp reduction, if not total absence, of a functional metakinetic bending plane, despite the presence of the cartilaginous ascending process of the tectum synoticum. The post-orbital bar is incomplete and according to Leonard (1973) this is a prerequisite for mesokinesis. Smit (1964) agrees that metakinesis is reduced or absent and states that movement is clearly possible between the parietal and the frontal bones, indicating that the *Typhlosaurus* skull is definitely mesokinetic.

Jaw mechanics

According to Ostrom (1964) the vertebrate lower jaw operates as a lever of the third class during adduction. This arrangement ensures maximum depression of the jaws with a minimum length of adductor muscle fibres. In a system of this kind the mechanical advantage is directly proportional to the length of the moment arm if the applied force (adductor musculature) remains constant. The moment arm is defined as the perpendicular distance between the line of applied force and the fulcrum (Fig. 18A). In the jaw the moment arm represents the distance between the jaw articulation and the tip of the coronoid process.

If the line of applied force functions in a posterior direction, at an angle of less than ninety degrees to the long axis of the lever, the moment arm FB (Fig. 18A) is no longer perpendicular to the applied force and is effectively displaced to position FB′ (Fig. 18B) with the result that the length of the moment arm is decreased and the system functions at a disadvantage. However, this condition can be overcome by raising the point of attachment (development of a coronoid process) of the applied force (Fig. 18C).

From Figure 18C it follows that: $m^2 = x^2 + y^2$.

The moment arm (m) is therefore a function of x (the distance between the coronoid process and the jaw articulation) and y (the height of the coronoid process). If y is constant x will determine the line of muscle action (θ) and vice versa, because $\tan \theta = \frac{y}{x}$.

Consequently, with y constant any decrease in x will result in a more posteriorly directed line of muscle action, or, alternatively, an increase in x will result in a more perpendicular orientation of the adductor fibres. If x is kept constant and y decreased the fibre orientation would become more vertical

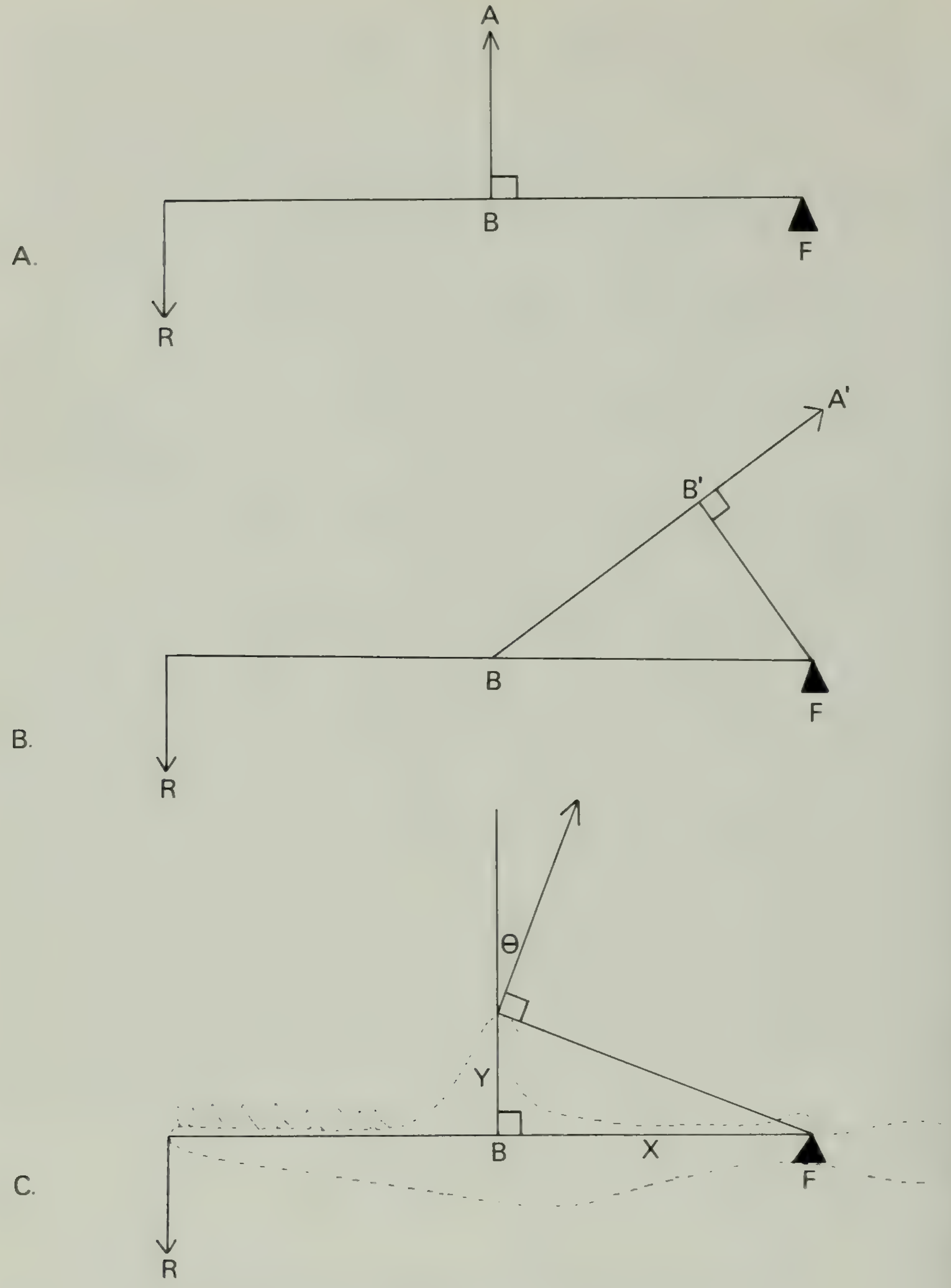

Fig. 18. Diagram to illustrate the action of the lower jaw.

and if y is increased the fibre orientation would become more posteriorly directed. It is clear therefore that the coronoid process in terms of height (y) and distance from the articulation (x) is functionally important in determining the action of the lower jaws and its associated musculature, and not as De Weerdt (1971) suggests, mainly a strengthening device.

The vertebrate lower jaw, seen in terms of the mechanics of a third class lever, would theoretically function at optimal efficiency with the adductor fibres orientated perpendicular to the long axis of the lower jaw and inserted on to the jaw as close as possible to the symphysis.

Ostrom (1964) notes two disadvantages in this arrangement. As a result of increasing x the gape of the mouth will correspondingly decrease. However, De Mar & Barghusen (1973: 626) state: 'If the increase in relative lengths of the moment arms achieved by increasing y and increasing x are the same, the increase in distance that the muscle must stretch to achieve a given gape is the same for the two methods. Thus . . . reduction of gape is the same and not a consideration *per se* in making the comparison.'

Secondly, Ostrom (1964) indicates that because of their vertical orientation the origin of the adductor fibres would encroach on to the facial region, restricting their size and power. This statement is true except in cases where the orbit is anteriorly placed or decreased in size, making it possible to extend the temporal origin of the jaw adductors anteriorly. In *Typhlosaurus* the eye is degenerate and lacks eye muscles. The orbit is consequently reduced and the temporal region elongated. The lateral downgrowth of the parietal and the forward extension of the anterior superior process of the pro-otic makes additional areas of origin available for the adductor musculature, compensating for the loss of such structures as the supratemporal arch. The relatively forward position, therefore, of the adductor muscles suggests a difference in the line of muscle action as compared to a non-fossorial skink like *Mabuia*.

From the work of De Mar & Barghusen (1973) it is clear that the height and position of the coronoid process is influenced by the line of muscle action. Any difference, therefore, in the line of muscle action would be reflected in the proportions of the lower jaw.

In comparing the lower jaws of *Typhlosaurus* and *Mabuia* the outstanding feature is their proportional similarity in terms of x and y. The tooth row, however, is shorter in *Typhlosaurus* than in *Mabuia* because of the subterminal mouth of the former. Consequently, the force of the bite at the jaw symphysis will probably be proportionately greater in *Typhlosaurus* than in *Mabuia*. The similarity of the two lower jaws suggests that the mean line of muscle action is identical in both forms, and that there is probably no difference of any consequence in the action of the jaw.

It therefore appears that the primary adaptation for a fossorial habit is streamlining of the body and its various parts. Loss of limbs and attenuation of the body is associated with the new mode of locomotion. Strengthening of the skull for burrowing results in the lateral downgrowth of the parietal bone and the extension of the anterior superior process of the pro-otic bone, the lengthening of the temporal region, and the loss of metakinesis and the supratemporal arch.

It may be concluded therefore that the distribution of the jaw muscles in *Typhlosaurus* represents the optimal functional arrangement to maintain a mode of jaw action essentially similar to that of a non-fossorial lizard such as *Mabuia capensis*, within a skull that is proportionally different because of marked changes resulting from a fossorial mode of life.

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*Not seen in the original.

ABBREVIATIONS

ac	anterior process of the coronoid
aem	m. adductor mandibulae externus medius
aep	m. adductor mandibulae externus profundus
aes	m. adductor mandibulae externus superficialis
aip	anterior inferior process of the pro-otic
ap	m. adductor mandibulae posterior
ar	articular
asp	anterior superior process of the pro-otic
at	stapedial artery
ba	bodenaponeurosis
bc	buccal cavity
bl	buccal lining
bo	basioccipital
bp	basipterygoid process
br	brain
bt	basal tuberosity
c	coronoid
cc	m. constrictor colli
ci	internal carotid artery
cm	m. cervicomandibularis
cp	coronoid process
d	dentary
dma	anterior portion of the m. depressor mandibulae
dmp	posterior portion of the m. depressor mandibulae
e	eye
em	m. episternocleidomastoideus
ex	extracolumella
gg	Gasserian ganglion
ggl	m. genioglossus
ghl	m. geniohyoideus lateralis
ghm	m. geniohyoideus medialis
gp	groove for the insertion of the pseudotemporalis muscle
fa	fascia supporting the extracolumella anteriorly
f	pad of fibrocartilage
fc	foramen for the chorda tympani
hg	m. hyoglossus
ia	m. intermandibularis anterior
if	infraorbital fenestra
ip	m. intermandibularis posterior
it	insertional tendon of the m. cervicomandibularis
itp	insertional tendon of the m. pterygoideus
lb	lateral lamina of the bodenaponeurosis
lc	m. longus colli
lca	m. longissimus capitis
lce	m. longissimus cervicis
ll	longitudinal lingual fibres
lp	m. levator pterygoidei
lq	lateral lamina of the quadrate tendon
ls	lateral semicircular canal
lv	lateral head vein
m	musculus
mb	medial lamina of the bodenaponeurosis
me	Meckelian cartilage
mq	medial lamina of the quadrate tendon
ms	lateral mandibular shelf
nl	nuchal ligament
oc	m. obliquus capitis magnus

oe	fused ophistotic-exoccipital
p	m. pseudotemporalis
pa	pre-articular
pal	palatine
par	parietal
pat	ascending process of the tectum synoticum
pb	parasphenoid—basisphenoid
pc	posterior process of the coronoid
pd	tendinous pad on m. pterygoideus
pe	lingual process
pf	postfrontal
pm	posterior mylohyoid foramen
pn	palatine nerve
po	pro-otic
prp	m. protractor pterygoidei
pt	pterygoid
pts	m. pterygoideus
q	quadrate
qa	quadrate tendon
r	rostral
ra	m. rectus capitis anterior
rm	mandibular ramus of V
rma	maxillary ramus of V
rop	opthalmic ramus of V
rp	m. rectus capitis posterior
s	stapes
sa	surangular
sc	spinalis capitis
sd	m. spinalis dorsi
sp	splenial
sq	squamosal
st	supratemporal
t	tendinous sheath of the extra columella
tc	tendinous connection between supratemporal and quadrate
tl	tranverse lingual fibres
to	tongue
tr	trachea
ts	tendon between the squamosal and quadrate
vb	vertical lamina of the bodenaponeurosis
vl	vertical lingual fibres
vq	vertical lamina of the quadrate tendon

6. SYSTEMATIC papers must conform with the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. n., sp. n., comb. n., syn. n., etc.

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Family Nuculanidae

Nuculana (*Lembulus*) *bicuspidata* (Gould, 1845)

Figs 14–15A

Nucula (*Leda*) *bicuspidata* Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (figs 8a–b).
Nucula largillierti Philippi, 1861: 87
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9

Note punctuation in the above example:
comma separates author's name and year
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dash, not comma separates consecutive numbers

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Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33.51S, 25.39E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and of date.

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JURI A. VAN DEN HEEVER

THE CRANIAL AND CERVICAL MUSCLES OF THE SOUTH AFRICAN LIMBLESS LIZARD *TYPHLOSAURUS AURANTIACUS AURANTIACUS* PETERS (REPTILIA, SAURIA)

VOLUME 69 PART 9 APRIL 1976 ISSN 0303-2515

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Fischer, P.-H. 1948. Données sur la résistance et de le vitalité des mollusques.—*J. Conch., Paris* **88**: 100–140.
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Kohn, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon.—*Ann. Mag. nat. Hist.* (13) **2**: 309–320.
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continued inside back cover)

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THE PLIOCENE FOSSIL OCCURRENCES IN 'E' QUARRY, LANGEBAANWEG, SOUTH AFRICA

By

Q. B. HENDEY

Cape Town Kaapstad

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THE PLIOCENE FOSSIL OCCURRENCES IN 'E' QUARRY, LANGEBAANWEG, SOUTH AFRICA

By

Q. B. Hendey

South African Museum, Cape Town

(With 6 figures and 4 tables)

[*MS. accepted 27 November 1975*]

ABSTRACT

The Pliocene Varswater Formation in the vicinity of Langebaanweg, Cape Province, is comprised of three main units, now named the Gravel, Quartzose Sand and Pelletal Phosphorite Members. The lowest unit in the succession, the Gravel Member, has yielded a largely marine fauna, including fifteen shark species, incorporated in rocky and sandy beach deposits. The principal source of fossils, the Quartzose Sand Member, was laid down in a variety of depositional environments in and near an estuary. The economically important unit, the Pelletal Phosphorite Member, is fossiliferous in a relatively limited area which was situated in the immediate vicinity of the river mouth. The fossils from the deposits overlying the Gravel Member represent a wide variety of marine, freshwater and terrestrial invertebrates and vertebrates. About seventy-five mammalian species are recorded, including a few belonging to groups not previously recorded from Africa.

CONTENTS

	PAGE
Introduction	215
Geology	218
Depositional environments	222
Fauna	231
Flora	243
Dating	243
Conclusions	245
Acknowledgements	245
References	246

INTRODUCTION

Large-scale production of phosphate from deposits on the farm Langeberg near Langebaanweg, Cape Province, was commenced in 1953 and several years later the presence of fossils in these deposits was reported (Singer 1961). Initially few fossils of good quality were collected, but prospecting revealed the presence of highly fossiliferous deposits south of a small open-cast mine, 'E' Quarry. During 1964 these deposits were exposed in a trench about 240 metres long, 120 metres wide and ranging in depth from 2 to 30 metres (Fig. 1). Soon after the 1964 excavations were commenced it became apparent that the deposits would yield well-preserved fossils in large quantities. Mining of 'E' Quarry (the New Varswater Mine) has been continuous since then and although the number

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of fossils recovered has varied from year to year, the original expectations have been fulfilled. Certainly no other recorded African fossil occurrence of Pliocene age has produced so large an assemblage of specimens representing so wide a variety of species.

During 1968 the South African Museum commenced an investigation of the fossiliferous deposits exposed in 'E' Quarry, this project following on from a similar undertaking directed for a period of ten years by R. Singer of the University of Chicago. The first phase of the Langebaanweg project had also taken into account the mined-out occurrences at 'C' Quarry on the farm Langeberg and Baard's Quarry on the farm Muishondsfontein. The fossils from these sites are limited in both quality and quantity and there are some still unresolved problems relating to their geological associations.

Several publications have resulted from the second phase of the Langebaanweg project, including reviews (Hendey 1970*a*; 1973; 1974*a*), accounts of the geology (Tankard 1974*a*; 1974*b*; 1975), discussions on dating (Hendey 1970*b*; 1972*a*; 1974*b*), as well as descriptions of some of the fossils recovered (e.g. Simpson 1971; Kensley 1972; Gentry 1974).

The geological study of the 'E' Quarry deposits, which has now been largely completed, formed part of a broadly-based investigation of late Cenozoic deposits in the south-western and southern Cape Province, and was undertaken independently of the palaeontological study, although the two have been mutually complementary.

Recently research on the fossils from Langebaanweg has decreased, although there has been an increase in the amount of material collected. The latter development is a direct result of changes in the mining programme. The expected back-filling of 'E' Quarry (Hendey 1973) was commenced during 1974 and collecting was accelerated in those areas to be covered by new mine dumps. In addition, the mining company (Chemfos Limited) removed a large quantity of fossiliferous deposit from one of the threatened areas (East Stream, see Fig. 1) and this is being screened by the first permanent field assistants on site. The nature of the present undertaking is being further influenced by the fact that during 1975 mining of the last of the phosphatic deposits known to be highly fossiliferous was commenced. Until recently these deposits were not scheduled to be mined until about 1990.

Since its inception, the prime object of the present phase of the Langebaanweg project has been the recovery and identification of fossils, with the collecting being as comprehensive as possible. The recent changes in the mining programme have added urgency to this aspect of the undertaking since leisurely collecting and excavation over certain areas of the mine are no longer possible and the areas thus affected will increase with the passage of time. Many of the specimens still in the deposits will be lost if they are not salvaged promptly. In addition, the volume of fossiliferous deposit elsewhere is being steadily reduced by the mining and although some is likely to remain indefinitely, technical difficulties may make it inaccessible to further exploitation. The termination of active field

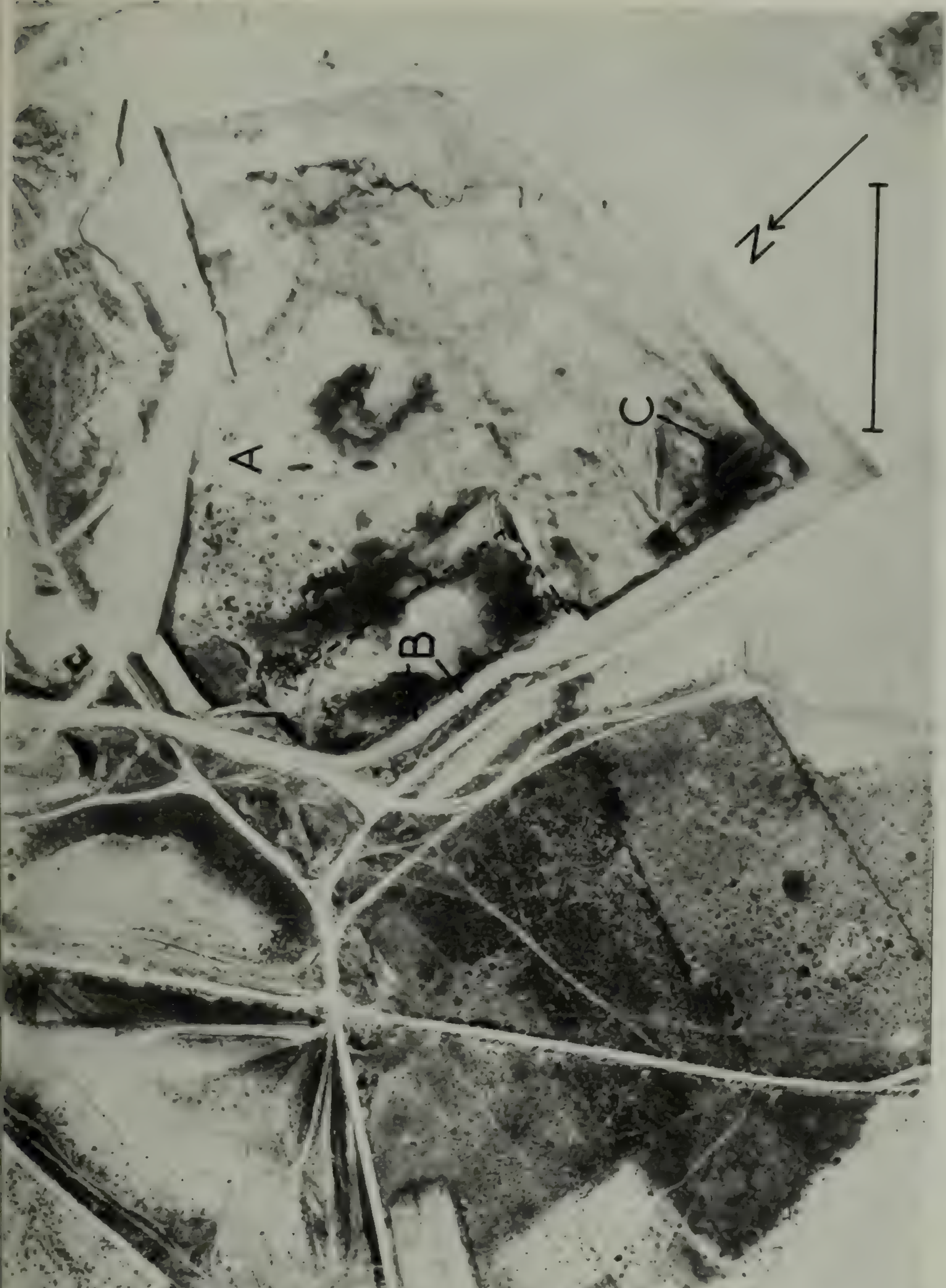

Fig. 1. Aerial view of 'E' Quarry, Langebaanweg (July 1974).
A. East Stream. B. Exposures of bed 3aS. C. Peat bed. Stippled lines around B indicate approximate extent of the 1964 excavation. D. The mined-out 'C' Quarry. Scale line approximately 250 metres.

work at the site in the not too distant future has now become a distinct possibility.

The collecting of fossils could be expedited by being more selective, but as far as possible this approach is avoided, mainly because it would adversely affect that part of the undertaking concerned with the recording of the nature of the fossil occurrences. This aspect of the investigation already suffers because of its lower priority rating. It is hoped that eventually an analysis of specimens from any given area in terms of species and body part representation, together with their condition and associations, will provide information on environments of deposition, the taphonomy of the fossils and aspects of the ecology of the area at the time of deposition. Some information of this nature is already available.

Although more time has recently been spent on the collecting of fossils and directly related technical matters, some progress has been made in the palaeontological research, and the present report updates some of the information and opinions previously recorded.

GEOLOGY

The phosphatic and fossiliferous deposits exposed in 'E' Quarry make up what is now termed the Varswater Formation (Hendey 1974*a*; Tankard 1975). This formation is Pliocene in age and it is underlain by the Miocene Saldanha Formation (Tankard in press). The overlying deposits, informally termed the 'surface bed', are largely, or entirely Pleistocene and Holocene in age. The Varswater Formation is comprised of three main units which were referred to by a variety of names in earlier publications. The member names used in the present report (Table 1) are those which are now considered most appropriate (A. J. Tankard pers. comm.), while those of the beds are purely informal and likely to be modified at a later date. The Gravel and Pelletal Phosphorite Members are both unequivocally described by their names, but the name of the Quartzose Sand Member refers to the dominant lithological element. This member also includes horizons of carbonaceous sand and clay (the 'peat bed', Fig. 1), clayey sands and silt. The non-geographic names of the members are justified in terms of Section 3.10(*d*) of the South African Code of Stratigraphic Terminology and Nomenclature (1971: 118).

Since Tankard (1975) has described the Varswater Formation in detail, the only other comments on the geology of 'E' Quarry which are included here are those which have a bearing on the palaeontology of the deposits.

The Quartzose Sand Member is the most highly fossiliferous of the three units, while the Pelletal Phosphorite Member is poorly fossiliferous, except for an area still exposed of the west wall of the mine ('bed 3a', Fig. 1). There are only limited exposures of the Gravel Member in a few areas of the mine and relatively little attention has been paid to this unit during the current phase of the Langebaanweg project.

Table 1

Stratigraphy of the 'E' Quarry exposures of the Varswater Formation

	Hendey (1974)	Tankard (1975)	Present report	
			MEMBERS	BEDS
VARSWATER FORMATION	Bed 3	Pelletal Phosphorite Member	Pelletal Phosphorite Member	beds 3aS & 3aN (fossiliferous) and other unnamed beds
	Bed 2	Fluvial Sand Member	Quartzose Sand Member	tidal mud flat bed, peat bed and other unnamed beds (fossiliferous)
	Bed 1	Beach Gravel Member	Gravel Member	—

Over most of 'E' Quarry the three members of the Varswater Formation are readily identifiable. The Gravel Member is always unmistakable, although the sandy element of this member may on occasion have been regarded as part of the overlying Quartzose Sand Member. Recognition of the Pelletal Phosphorite Member has, for the most part, not been difficult, although its lower limit has not always been clearly defined. The problems encountered in recognizing the lower limit of this member have been due to a variety of factors. Theoretically the mining is cut off at the base of the Pelletal Phosphorite Member, although in practice this is impossible and irregularities on the floor of the mine do not necessarily reflect the nature of the boundary between the Pelletal Phosphorite and Quartzose Sand Members. In most areas the mining has actually extended into the latter unit where the exposed surface may be contaminated and obscured by spillage from the excavator and slumping of deposit from the vertical mine faces. Furthermore, the Quartzose Sand Member was truncated prior to the deposition of the Pelletal Phosphorite and where it is very thin it has been difficult or impossible to recognize. In certain critical areas the deposits of the two members are superficially similar and although detailed sediment analyses would no doubt resolve the issue in problematical instances, no such analyses have been undertaken.

From the preceding comments it should be clear that difficulties have centred largely on the identification of the upper and lower limits of the Quartzose Sand Member. Added to this is the fact that this member is the most complicated unit in the succession in terms of lithology and the variable character of the deposits has itself led to some confusion in the past. The sometimes striking differences

Table 2

The stratigraphy of the East Stream and peat areas of 'E' Quarry

		EAST STREAM	PEAT AREA
VARSWATER FORMATION	PELLETAL PHOSPHORITE MEMBER	Phosphatic sand (? non-fossiliferous)	Phosphatic sand (? non-fossiliferous)
	QUARTZOSE SAND MEMBER	Quartzose sand (vertebrates common)	Silt (invertebrates common)
			Peat (vertebrates common)
	GRAVEL MEMBER	Sand & gravel (marine fossils common)	Sand & gravel (marine fossils common)

in the nature of the Quartzose Sand Member are illustrated by examples of the 'E' Quarry succession given in Table 2.

The difficulty experienced in identifying the units of the Varswater Formation has resulted in some of the fossils collected being of doubtful provenance. In this connection it should also be noted that before the basic three-unit succession was recognized in 1969, little or no data on the source of specimens was recorded and the provenance of many specimens collected before that date may never be known. The same often applies in the case of specimens picked up by mine workers. Although the problem of unprovenanced material is not as serious as it might have been, it is an unfortunate complication in the palaeontological investigation.

In the faunal lists given later, records of unknown or uncertain origin are excluded. The source of most of the more significant specimens from 'E' Quarry is well documented and all the species identified to date are represented by at least one specimen of known provenance.

The characteristics of the units comprising the Varswater Formation are accounted for by the sequence of events which occurred during deposition of the formation. These events have a direct bearing on the interpretation and identification of depositional environments (*vide infra*). They were summarized by Tankard (1974*a*: 219) who stated that, 'In the Pliocene a transgressing sea pushed deltaic marsh sediments ahead of it until it reached a temporary stillstand . . . [with the] temporarily stable conditions [allowing] a barrier bar to build up, behind which estuarine conditions prevailed. The estuary was fed by a river from the north-east. The final transgression reworked the older sediments.' It was at the time of the stillstand that the Quartzose Sand Member was accumulated, while the Pelletal Phosphorite Member was laid down during the final transgression (Fig. 2).

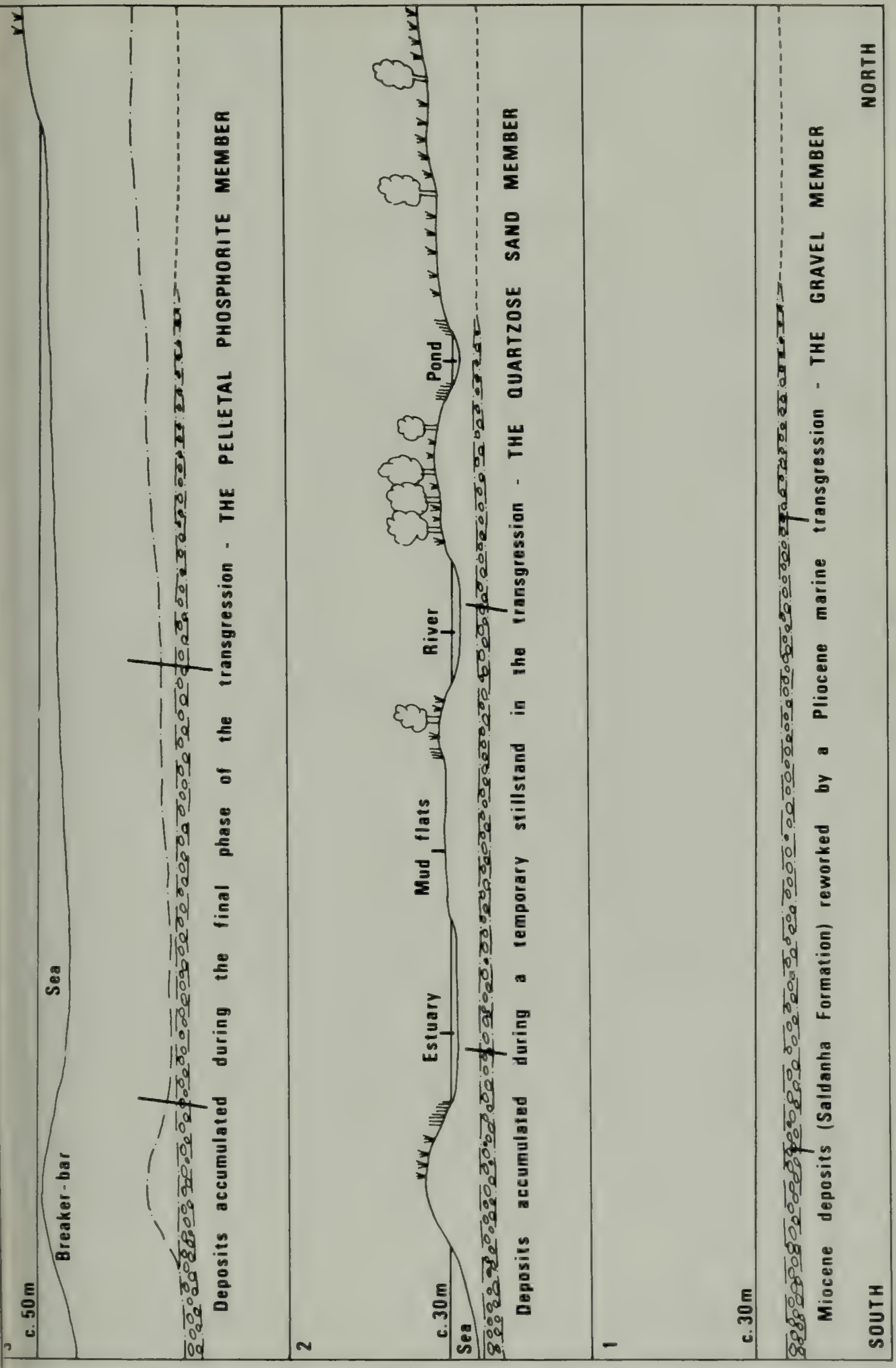
3
c. 50m
Breaker-bar
Sea
Deposits accumulated during the final phase of the transgression - THE PELLETAL PHOSPHORITE MEMBER
2
c. 30m
Sea
Estuary
Mud flats
River
Pond
Deposits accumulated during a temporary stillstand in the transgression - THE QUARTZOSE SAND MEMBER
1
c. 30m
Miocene deposits (Saldanha Formation) reworked by a Pliocene marine transgression - THE GRAVEL MEMBER
SOUTH
NORTH

Fig. 2. The depositional history of the Varswater Formation.

Although the geology of the Varswater Formation is now well known, there is still scope for further detailed work. Of particular interest to the palaeontological investigation is geological evidence indicating depositional environments. The relationships between fossils and the deposits in which they occur has hitherto received little attention.

DEPOSITIONAL ENVIRONMENTS

It is now generally accepted that the Varswater Formation accumulated during a marine transgression at a time when a river discharged into the sea in the immediate vicinity of 'E' Quarry. It follows that marine, fluvial and terrestrial environments were then present in the area, together with some of the attendant micro-environments peculiar to each. Theoretically it is therefore possible that deposition of this formation took place in more than one of these environments and also that as the sea transgressed macro- and/or micro-environmental changes might have occurred in any given area now exposed in the mine.

Tankard (1975) has given an account of the depositional environments of the three units comprising the Varswater Formation in 'E' Quarry. They were as follows:

Gravel Member—Rocky and sandy marine beach environments.

Quartzose Sand Member—Essentially estuarine and fluvial environments, although a peat deposit, probably representing a marsh environment, is also mentioned.

Pelletal Phosphorite Member—A shallow-water environment situated between a beach bar and beach.

The means by which the vertebrate fossils in deposits overlying the Gravel Member came to be incorporated in these deposits has been the subject of some dispute in the past (Tankard 1975: 281). There is in fact no single answer to this question and it is clear that just as the depositional environments of the sediments varied, so too did those of the fossils. The characteristics of the deposits change both vertically and horizontally, the most noticeable and frequent changes being in the lower levels of the succession, that is, those levels in which fossils occur most commonly. Although no detailed study of the relationships between sediments and fossils has yet been undertaken, it is obvious that differences in the deposits go together with palaeontological differences.

Some observations on the environments in which the 'E' Quarry fossils were laid down have already been recorded (Hendey 1974*a*), but it is probably worth while at this stage to elaborate on earlier statements.

The Gravel Member

The fauna of the Gravel Member is comprised overwhelmingly of marine species, both invertebrates and vertebrates, and the fossils of this member were undoubtedly accumulated along a marine shoreline. The invertebrates indicate the presence of both rocky and sandy habitats. Remains of terrestrial vertebrates do occur, but they are invariably fragmented and rolled. This also applies to many of the marine fossils. The condition of the fossils is evidently the result of wave action and it differs from that of fossils from fluvial deposits in the Quartzose Sand and Pelletal Phosphor te Members.

The Quartzose Sand Member

The situation in respect of Quartzose Sand Member depositional environments is complicated. Tankard (1975) has recognized both estuarine and fluvial facies within this member and many of the fossils recovered from the 'E' Quarry exposures must have been deposited in the river and estuary. For example, some of the fossiliferous exposures in the eastern parts of the mine are medium to coarse sands which are a westerly extension of the fluvial deposits referred to by Tankard (1975: 274). On the other hand, the nature of some fossil occurrences suggests that specimens were deposited in areas adjacent to the river and estuary in both subaerial and subaqueous situations (e.g. floodplain and pond).

Evidence suggesting that certain of the Quartzose Sand Member fossils were accumulated on land surfaces has been mentioned elsewhere (Hendey 1974*a*: 349–353). Since this discussion related to carnivore activity rather than environments of deposition, some points concerning the latter were omitted or insufficiently emphasized.

In certain of the Quartzose Sand Member exposures (e.g. the floodplain deposits of East Stream) the condition of the fossils and the nature of their occurrence contrasts with the situation where there is incontrovertible evidence for subaqueous deposition of material (e.g. in the fluvial deposits of the Pelletal Phosphorite Member). The fossils in the latter deposits tend to be abraded and fragmented, while elements of single skeletons are dispersed. Exceptions to these rules were probably specimens which had been protected by soft tissues or which had not been subjected to prolonged transport. The fossils of subaerially accumulated assemblages are generally perfectly preserved and damage to, or dispersal of, specimens can usually be ascribed to carnivore activity or fires.

The fact that there are certain Quartzose Sand Member fossil occurrences where only terrestrial species are recorded, or where they are much more commonly represented than aquatic species, also tends to suggest that there was subaerial accumulation of specimens. The presence of some aquatic species could be explained by periodic inundations of land surfaces. The persistent presence of an aquatic environment would lead to higher proportions of aquatic species being represented and there are occurrences in the Quartzose Sand Member where this is the case. In one such occurrence in the East Stream area a relatively high proportion of fish bones went together with appreciable quantities of abraded bone. These fossils were probably deposited in a channel, a feature for which there was no other obvious evidence.

An example of burnt bone having suggested that a skeleton cannot have been moved after it was partially burnt was given elsewhere (Hendey 1974*a*:

351). The nature of this particular occurrence was the important factor, since burnt bone itself is not necessarily proof that there were fires over areas presently exposed in the mine. Burnt bone might easily have been washed in from elsewhere. There is another recently discovered example of burnt bone which must have been *in situ*. This was a concentration of several hundred bones of small vertebrates, mainly rodents and insectivores, most of which are heavily charred. This occurrence is likely to represent the residue of a burnt owl pellet accumulation, which cannot have been moved after burning without the bones becoming dispersed.

A hitherto unrecorded factor which supports the theory that some subaerial accumulation of fossils occurred concerns the presence of coprolites in the deposits. Coprolites of at least three types have been recovered from the Quartzose Sand Member. The first and largest type were evidently produced by large carnivores, probably hyaenas. The second type are smaller and contain fragmented bones belonging to small vertebrates. They were probably produced by one or more of the smaller carnivores recorded from this member. An account of such coprolites was recently given by Mellett (1974). The last type are small, with no visible bone and tending to be cylindrical when not deformed. Their source is not known but they are extremely abundant in certain areas (e.g. East Stream).

Coprolites have been recovered only in certain parts of the mine and, except for the smallest kind, they are nowhere common. Their condition varies, some being remarkably fresh in appearance, while others are fragmented and distorted. One of the ?hyaena coprolites, which was found together with four others, is flattened, its appearance suggesting that it was trampled when fresh. Some of the smallest coprolites, which are very fine-textured, show clear impressions made by leaves, although they may be otherwise undistorted.

In order for faeces to be preserved intact they must almost certainly have been dropped on a land surface and have been fairly rapidly buried thereafter. Fresh faeces dropped in and then transported by water is unlikely to have survived intact for long. It is also unlikely that groups of specimens would have remained together if they had been transported and there are four instances recorded where groups of 3, 3, 5 and 7 ?hyaena coprolites were found in close association. These groups, together with several isolated specimens, came from a relatively limited area in the eastern part of the mine. Unexcreted faeces could have been carried to its final resting place while still inside a carcass, but none of the coprolites has been found in direct association with other remains of their possible producer. In addition, the shape of the better preserved specimens, and the presence of leaf impressions on some, indicates that they had actually been excreted.

Taken in conjunction the various factors referred to above are here regarded as convincing evidence for subaerial accumulation of at least part of the Quartzose Sand Member fossil assemblage.

The earlier reference to periodic inundations of land surfaces was intended to indicate seasonal flooding of the river and estuary, but there is also evidence for tidal flooding. A recently exposed deposit in the south-western part of the mine includes an invertebrate fauna which indicates that the depositional environment was a tidal mud flat. The nature of the deposits is in keeping with the fauna which it contains. The limited exposures of this deposit examined prior to their becoming temporarily inaccessible suggested that it overlies the peat bed mentioned earlier (see Table 2).

The faunas of the peat and tidal mud flat beds are strikingly different from one another and both differ from the fauna of more typical exposures of the Quartzose Sand Member elsewhere. The mud flat bed is an exceptional occurrence in this member, being the only one from which large numbers of well-preserved invertebrate fossils have been recovered. Vertebrate remains are rare. By contrast vertebrate fossils occur commonly in the peat bed and in certain other exposures of the Quartzose Sand Member. As fossil-collecting in this member has progressed, it has become apparent that while certain vertebrate species are fairly ubiquitous, others occur only in certain areas, while the overall representation of species and the condition of specimens varies from place to place. While it may not yet be possible to interpret all such evidence meaningfully, a superficial comparison of the peat bed and East Stream faunas should serve to illustrate that different sediments go together with faunal differences.

In this instance the sediment differences are visually striking, the black sands and clays of the peat bed contrasting sharply with the white quartzose sands of the East Stream area. The deposits in the latter area are here regarded as a largely floodplain accumulation, while the peat area is thought to have been a marsh.

The fossils of the peat bed tend to be less complete than those from East Stream, although this may in part, or even largely, be due to the recent disturbance of the peat by mining activities. This disturbance may also account for the fact that whereas at East Stream a number of instances are recorded where partial skeletons of individuals were preserved, nothing on a comparable scale has so far been observed in the peat bed. A notable exception was the discovery of the distal extremities of a sivathere fore- and hindlimb, elements of which were found in articulation standing more or less vertically in the deposit, seemingly all that survived of an animal trapped in the marshy deposits. At East Stream elements of single skeletons were, with few exceptions, found slightly dissociated from one another and they tended to lie more or less horizontally in the deposits. This suggests that they were accumulated on a firm surface.

Although a single species of land tortoise (*Chersina* sp.) is the most commonly represented vertebrate in both areas, there are otherwise some marked differences in the representation of species. There are many species recorded from East Stream which are not known from the peat bed, although the reverse either does not apply or is at least much less obvious. Another example concerns the pig, *Nyanzachoerus*, which is known from the peat bed on the basis of only a few isolated teeth and bones, whereas at East Stream the remains of at least fifteen individuals, some represented by incomplete skeletons, have been collected. Birds, which are common in both areas, provide another example. In the East Stream assemblage the most common species is a francolin, which is a terrestrial bird, but in the peat bed it is rare, while waterbirds are relatively more common (G. Avery pers. comm.).

Another rather curious difference between the two faunas concerns the representation of the seal, *Prionodelphis capensis*. This species is not common in either of the faunas, but at East Stream it is represented almost exclusively by the remains of very young individuals, whereas only a few isolated teeth and bones of adult seals are known from the peat bed. There are also differences in the coprolite occurrences in the two areas. East Stream is one of the areas in the mine where the smallest type of coprolite occurs in great numbers, while the larger type with visible bone and those of ?hyaenas are rare. The only coprolites known from the peat bed are a few specimens of the type which contains visible bone.

A complete analysis of the two assemblages will no doubt provide further and more precise examples of their similarities and differences, which are presumably more than just fortuitous.

The potential importance of faunal analysis in determining depositional environments is illustrated by the fact that there are obvious differences in faunal assemblages even where deposits are superficially little different or indistinguishable. Such differences have been observed at the same level in apparently homogeneous deposits over distances of only a few metres. An example mentioned earlier was the occurrence in the East Stream area of a 'channel' containing a relatively high proportion of fish remains and abraded bones. A second example concerns a quartzose sand exposure in the vicinity of the peat bed which was found on screening to contain large numbers of frog bones, but very few terrestrial vertebrate fossils. In similar deposits elsewhere the representation of fossils was reversed, with frogs being rare and terrestrial vertebrates common. The presence of a pond, which left no other obvious traces, could account for the amphibian-rich occurrence.

Although the question of depositional environments within the Quartzose Sand Member has received only passing attention during the current phase of the palaeontological investigation, there is evidence for fossils having accumulated in estuarine, fluvial, marsh, mud flat, pond and floodplain environments.

The Pelletal Phosphorite Member

The Pelletal Phosphorite Member covers a wide area and is much the thickest of the units in the Varswater Formation, but it is known to include vertebrate fossils in large numbers only in a relatively limited area, exposures of which still exist along the more northerly part of the west wall of the mine. These fossiliferous deposits are informally termed 'bed 3a' and reasonably large fossil samples have been recovered from two exposures, designated 'bed 3aS' and 'bed 3aN' (Fig. 3).

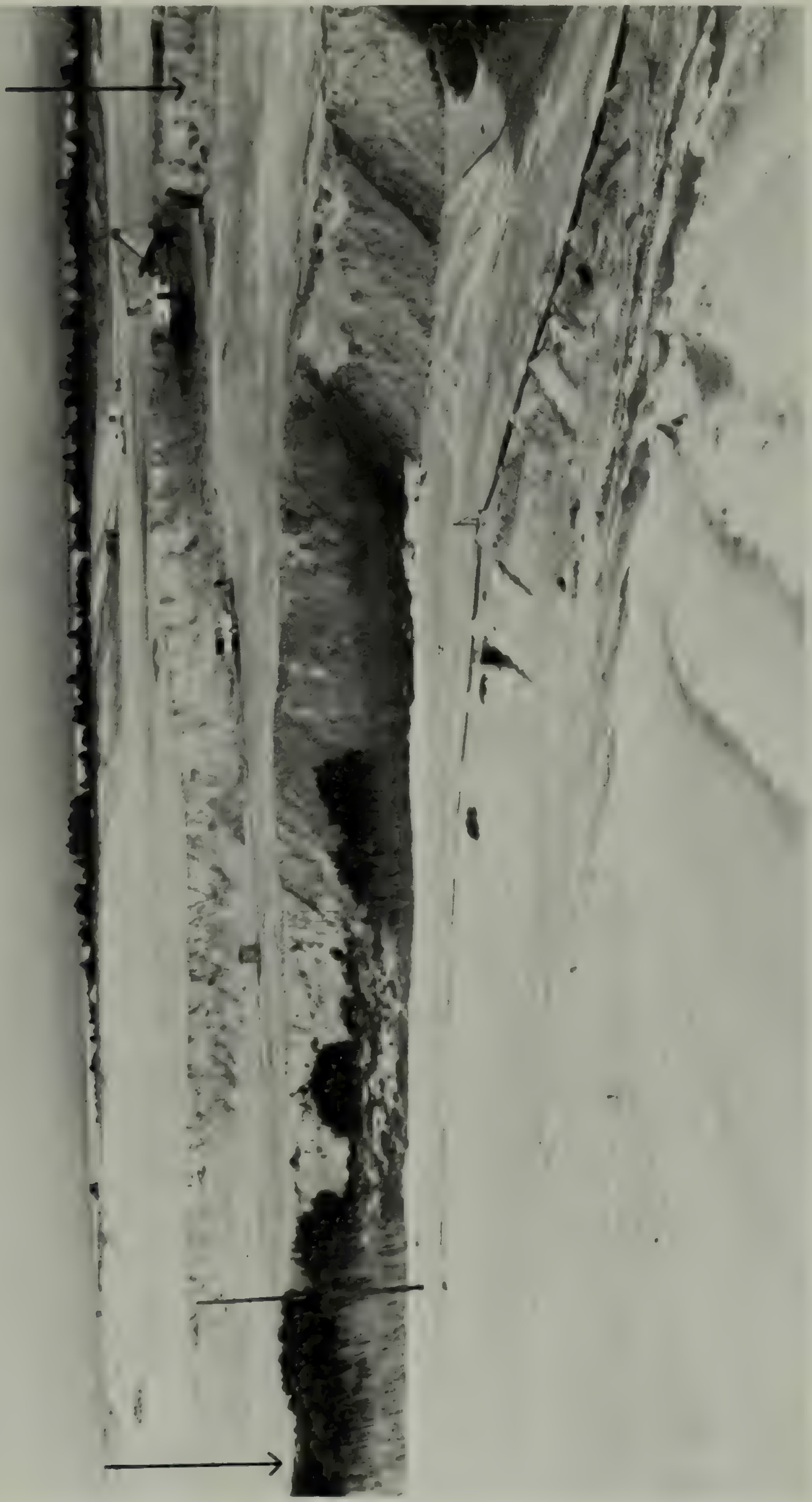

Fig. 3. The new westerly extension to 'E' Quarry (August 1975), showing exposures of bed 3aN (arrowed right) and bed 3aS (arrowed left, behind trees).

The bed 3aS deposits are exposed along the lower mining face ('bottom cut') of the west wall, while the bed 3aN deposits are approximately 100 metres north-north-west on the upper mining face ('top cut') at elevations of between 2 and 4 metres higher. The bed 3aN deposits are close to the northerly limit of economically recoverable phosphate and are only between 2 and 3 metres thick, of which only the lowest 0,5 to 1 metre is fossiliferous. Some fossils have been recovered from the uppermost levels of the Pelletal Phosphorite in this area, but they are not regarded as part of the bed 3aN sample. The bed 3aS deposits are also between 2 and 3 metres thick in an area sampled by controlled excavations during 1969 and 1970. In this area fossils were concentrated in three distinct levels spread over the lowest 1,5 metres of deposit. Bed 3aS deepens in a southerly direction, where there may be more than three levels of concentration. The thickness of both beds 3aS and 3aN is considerably less than the 25 metre maximum development of the Pelletal Phosphorite Member.

In the bed 3aN area the base of this member is marked by a 0,75 metre thick phosphatic sandstone. The surface of the rock at its most northerly exposure appears to be fairly smooth and more or less horizontal, while the overlying deposits are apparently not fossiliferous. A little further south the rock surface dips markedly to the south-west and it becomes progressively more irregular. Crevices and potholes filled with coarse sand and gravel are common and the rock eventually becomes discontinuous. Fossils occur in abundance where the rock surface is irregular, being concentrated in the irregularities and becoming progressively less common upwards in the overlying finer-grained sediments. The latter have a clay component in the more northerly exposures, but this is absent in the southerly exposures where the deposits which immediately overly the rock are unconsolidated sands. The ill-defined boundary between these two types of deposit runs from north-east to south-west. Indications are that there was a channel of fast-flowing water directed in a south-westerly direction in that area where the rock surface is irregular and where the overlying deposits are unconsolidated sands. The clayey-sands apparently formed the northern bank of the channel.

The nature of the bed 3aS fossiliferous occurrences is essentially similar, except that in this instance there is no rock horizon at the base of the deposits, there are no clayey deposits indicating a channel bank and fossils are concentrated at more than one level in the deposits. The exact stratigraphic relationship between bed 3aS and bed 3aN is not known, but the lower elevation and more southerly situation of the former suggests that it was laid down earlier during the marine transgression than bed 3aN. There may, however, be a direct link between the highest of the bed 3aS levels of fossil concentration and bed 3aN.

Indications are that bed 3a was laid down in, or in the direct path of the river which discharged into the sea most of the sediment making up the Pelletal Phosphorite Member and that the course of the river shifted northwards as the sea transgressed. A structure contour map of the base of the Pelletal Phosphorite Member (Tankard 1975: fig. 3), a modified version of which is reproduced here

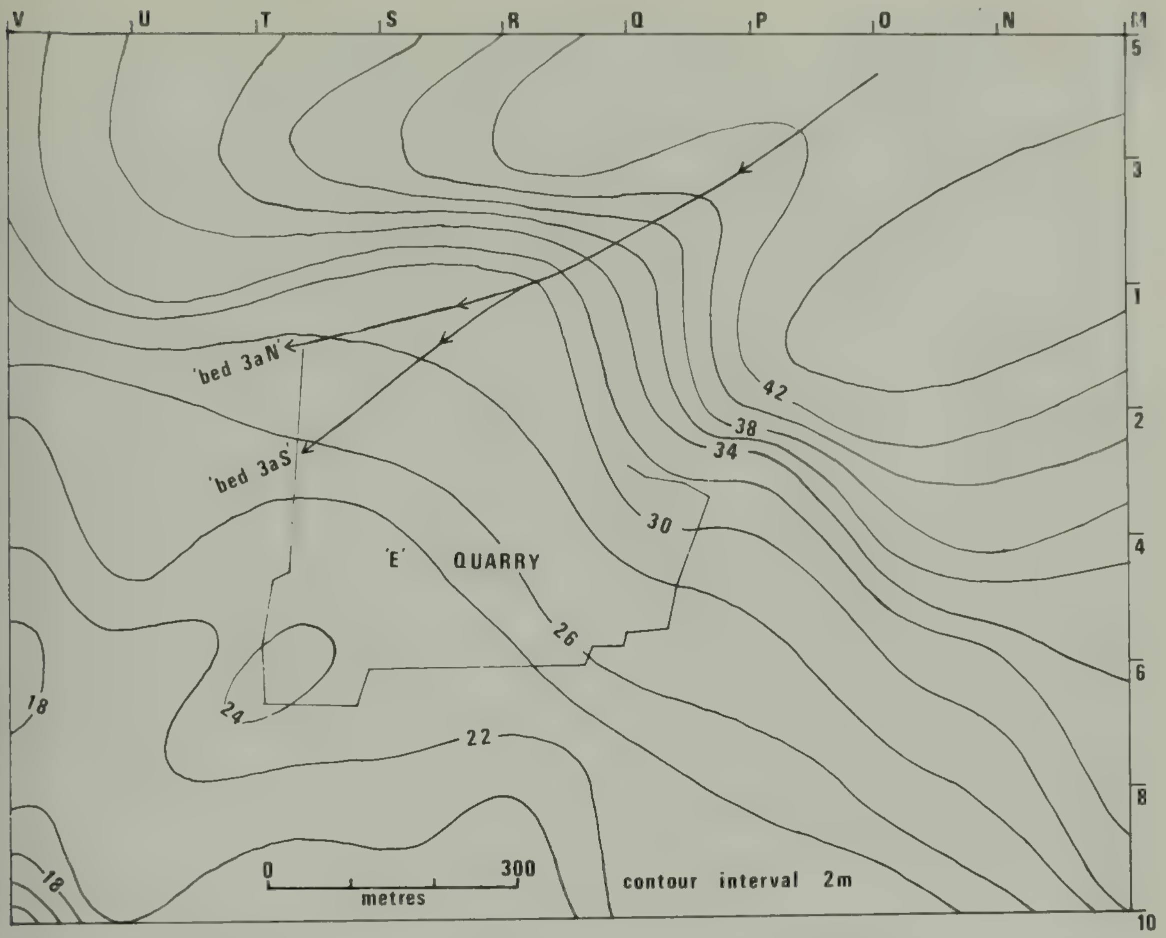

Fig. 4. Structure contour map of the base of the Pelletal Phosphorite Member. Arrowed lines indicate the probable courses of the river at the time that beds 3aS and 3aN were laid down. (Adapted from Tankard 1975: Fig. 3.)

(Fig. 4), supports the suggestion that the lower course of the river was directed towards the area where bed 3a is now exposed.

The nature of the bed 3a fossil occurrences, and particularly those of bed 3aN, provide clear evidence for deposition by fast-flowing water. Specimens trapped by irregularities in the rock surface had protruding parts either completely abraded away or broken up and the fragments scattered in a south-westerly direction. In many instances specimens on the rock surface had their lower parts abraded, apparently by the coarser sediment fraction carried along the rock surface by the flowing water. Individual elements of single skeletons were dispersed and in some instances were traced by following connected series of irregularities in the rock surface.

A feature of the faunas of both beds 3aS and 3aN was the large number of specimens of the seal, *Prionodelphis capensis*, which are represented. Several well-preserved skulls of this species were recovered from bed 3aN, while the several skulls of the similarly-sized hyaena, *Hyaena abronia*, found in the same deposits were not as well preserved or as complete. The more numerously represented and better preserved remains of the aquatic carnivore suggests that deposition was in a subaqueous environment and that the remains of the terrestrial species had suffered transport over longer distances. As a general rule the terrestrial fossils from bed 3a are more fragmented and less well preserved than similar specimens from some of the Quartzose Sand Member deposits.

While most of the bed 3a fossils probably were deposited subaqueously, the possibility cannot be ruled out that some subaerial accumulation of material also took place (e.g. on the river banks and/or sand bars). A ?hyaena coprolite was recovered from the clayey deposits of bed 3aN, that is, those deposits regarded as having formed the northern bank of the channel at the time that the fossils of bed 3aN were being accumulated. The smallest type of coprolite is not uncommon in bed 3aS, but the majority of these specimens are fragmented, their condition being in marked contrast to the generally very well preserved specimens from the Quartzose Sand Member.

The previously stated opinion that some of the fossils from what is now termed bed 3aS were derived from the Quartzose Sand Member (Hendey 1970*b*: 122), may be relevant to the question of the bed 3aS coprolites. These specimens could well be part of the derived element of the bed 3aS assemblage, having hardened sufficiently while incorporated in the Quartzose Sand Member to survive transport to, and redeposition in the Pelletal Phosphorite Member. On the other hand, they were in most cases not hard enough to survive the transportation intact.

While there is a strong likelihood that the bed 3aS deposits include fossils derived from the Quartzose Sand Member, there is no evidence to suggest that this was the case with bed 3aN. Truncation of the Quartzose Sand Member after the 30 metre stillstand must have been confined to the early stages of the final transgression, that is, the time when the lower levels of bed 3aS were being laid down. The great majority of the bed 3aS coprolites come from the lower levels. The relatively high elevation of bed 3aN virtually precludes the possibility of it containing fossils derived from the Quartzose Sand Member.

Occasional fossils have been recovered from exposures of the Pelletal Phosphorite Member other than beds 3aS and 3aN. Some specimens have been collected in the west wall area from deposits overlying bed 3a, including a few from the uppermost level. These specimens were probably also transported into the area by the river. Their rarity may be due to the river mouth having been some distance away when these deposits were laid down, the fossils representing the remnants of occasional carcasses which had floated out to sea from the river mouth. Specimens have also been collected from several different levels in the most north-easterly exposures of the Pelletal Phosphorite Member. These fossils are probably the remains of animals accumulated near the southern side of the river mouth, while those of bed 3a accumulated in, ahead of and on the northern bank of the river mouth (Fig. 4).

FAUNA

During the past six years large numbers of fossils have been collected from 'E' Quarry, most material having come from surface collecting, excavations at random and screening of deposit, but some also having been recovered in controlled excavations. The deposits sampled extend over an area of about 28 hectares (70 acres), with specimens having come from all the known fossiliferous horizons within the Varswater Formation. There is considerable variation in the size of assemblages from individual occurrences within the deposits, while the total assemblages from each of the three members are also of unequal size. The fauna of the Quartzose Sand Member is the largest and best known, since it has been exposures of this member which have been the principal focus of attention during the current phase of the Langebaanweg project (Fig. 5). Mining of highly fossiliferous Pelletal Phosphorite Member deposits (bed 3a) was recommenced during 1975 so that there has recently been a substantial increase in the amount of material collected from this member. Relatively little time has been devoted to the collecting of fossils from the Gravel Member, exposures of which are limited.

In terms of the requirements for taxonomic studies, many species, mainly amongst the smaller vertebrates, are more than adequately represented in existing collections and in such instances the addition of further material may be of little or no significance. There are, however, many more species which are poorly represented and in these instances there is still a real need to build up sample sizes. Since 1969 the annual additions to the collections have always included several new records for the site, while there has also been further identification of material already in the collections. The 'E' Quarry fauna is, in general, comparatively well known, although most of the specimens have still to be studied in detail.

The following summary accounts of groups represented in the fauna include references to recent new records, recent and current studies, significant additions to previously existing species assemblages, as well as other comments on available material.

Invertebrates

Many of the invertebrate fossils recovered from 'E' Quarry have already been described (Kensley 1972), this material having come from the Gravel Member, while Tankard (1975) has mentioned other invertebrates from the Varswater Formation. Additional material is now available, including the first substantial invertebrate assemblage from the Quartzose Sand Member. This material is from the tidal mud flat deposit mentioned earlier and includes marine, freshwater and terrestrial molluscs. Many of the specimens are remarkably well preserved, some even retaining traces of their original colour. This material is being studied by B. Kensley (South African Museum) and P. Nuttall (British Museum (Natural History)).

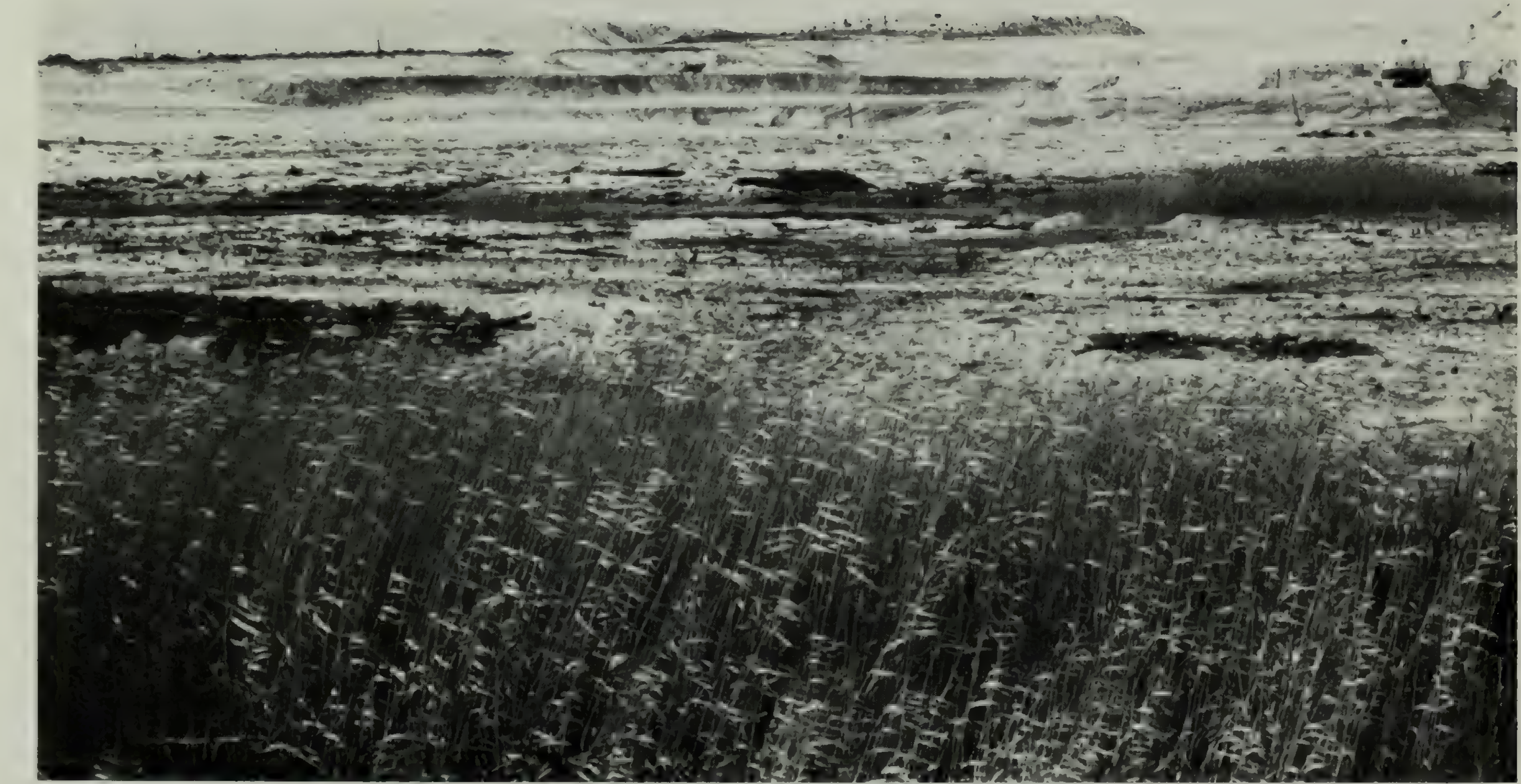

Fig. 5. A south-easterly view across 'E' Quarry. The Quartzose Sand Member is exposed over the floor of the mine, while the two lower vertical faces in the background are exposures of the Pelletal Phosphorite Member. The lighter deposit above the roof of the mechanical excavator on the right is the surface bed.

Lower vertebrates

No progress has been made in the identification of bony fish, amphibians and reptiles, but P. A. Hulley (South African Museum) has completed a preliminary investigation of the cartilaginous fish from the Gravel Member (Table 3). Of particular interest was the fact that the Selachii proved more diverse than anticipated, with the assemblage being complicated by the presence of derived specimens (see p. 243).

TABLE 3

A provisional list of the cartilaginous fish from the Gravel Member of the Varswater Formation, including derived material. (Identified by P. A. Hulley of the South African Museum.)

SELACHII
- Hexanchidae
  - *Notidanus serratissimus*
- Carcharhinidae
  - *Carcharhinus melanopterus*
  - *Carcharhinus limbatus*
  - *Galaeorhinus* sp.
  - *Prionace glauca*
  - *Negaprion* sp. or *Hypoprion* sp.
- Odontaspidae
  - *Odontaspis accutissima*
  - *Odontaspis* sp. B
  - *Odontaspis* sp. C
- Otodontidae
  - *Megaselachus megalodon*
- Carcharodontidae
  - *Carcharodon* sp.
- Isuridae
  - *Isurus* sp.
- Squalidae
  - *Squalus* sp.
- Squatinidae
  - *Squatina africana*
  - *Squatina* sp.

BATOIDEI
- Rajidae
  - *Raja* sp.
- Trygonidae
  - Gen. & sp. indet.
- Myliobatidae
  - *Myliobatis* sp.

Birds

Although the 'E' Quarry birds probably constitute the largest late Tertiary avian assemblage from anywhere in Africa, they have received only superficial attention, with only one species, a penguin, having been positively identified (Simpson 1971). The original study of the penguin remains suggested the presence of a second species and this has now been confirmed by more recently discovered material, although the second species remains unidentified (Simpson

1975). G. Avery (South African Museum) has identified to the family or genus level about a dozen other birds, but there are many more which are completely unclassified. The Quartzose Sand Member has been the source of the largest number and the best preserved of the specimens. New material includes incomplete skeletons of two large raptors and another belonging to a stork-like species. The tidal mud flat deposits of the Quartzose Sand Member contain fragments of bird egg-shell, some of which retain their colour.

Mammals

The mammalian fossils from the 'E' Quarry exposures of the Quartzose Sand and Pelletal Phosphorite Members have been the principal focus of the current phase of the Langebaanweg project. The number of species recorded from these deposits has grown steadily over the years and approximately seventy-five have now been positively or tentatively identified (Table 4). Only about one-third have been described and even these include a number which are incompletely classified, largely because of inadequacies in available material. In some instances newly discovered material has made positive identifications distinctly possible.

Mammalian microfauna

The updated list of 'E' Quarry mammals differs most markedly from those previously published by including provisional identifications of many of the small mammals from the Quartzose Sand Member. This part of the list was provided by T. N. Pocock (Vanderbijlpark, Transvaal). Of interest is the first record of a bat from the site. The small mammals of the Pelletal Phosphorite Member, which are generally represented by more fragmentary material, remain unstudied. The rodents are to be studied by Craig C. Black (Carnegie Museum, Pittsburgh).

Primates

Although a cercopithecoid is tentatively recorded, there has been increasing doubt about its presence in view of the continued lack of positively identifiable material. Primates feature prominently in the late Cenozoic fossil record of Africa and their great rarity in, or complete absence from the Varswater Formation is a perplexing aspect of its fauna. A feature of this fauna is its great diversity and the situation which exists in respect of so successful a group as the primates is indeed curious. The situation of Langebaanweg in a coastal environment at the southern continental extremity is likely to be related to the rarity or absence of this group. The Quaternary fossil record of the south-western Cape Province is characterized by a similar dearth of primates.

Carnivores

In contrast with the primates, carnivores are an exceptionally well represented and diverse group. Fully one third of the Varswater Formation mammals identified to date are carnivores.

TABLE 4

A provisional list of the mammals from the Quartzose Sand and Pelletal Phosphorite Members of the Varswater Formation.

	Quartzose Sand Member	Pelletal Phosphorite Member
INSECTIVORA		
Chrysochloridae		
Chrysochloris sp.	×	×
Soricidae		
Myosorex sp.	×	
Suncus sp.	×	
Soricidae gen. & sp(p). indet.		×
Macroscelididae		
Elephantulus sp.	×	×
CHIROPTERA		
Vespertilionidae		
Eptesicus sp.	×	
? PRIMATES		
? Cercopithecidae		
Gen. & sp. indet.	×	
PHOLIDOTA		
Manis sp.	×	
TUBULIDENTATA		
Orycteropus sp.	×	×
CARNIVORA		
Canidae		
Vulpes sp.		×
Ursidae		
Agriotherium africanum		×
? Procyonidae		
Gen. & sp. indet.	×	
Mustelidae		
Mellivora aff. *punjabiensis*		×
Mellivorinae gen. & sp. indet. (aff. *Plesiogulo*)	×	
Enhydriodon africanus		×
Viverridae		
Viverra leakeyi	×	×
Viverrinae gen. & sp. indet.	×	
Genetta sp.	×	
Herpestes sp. A	×	×
Herpestes sp. B	×	×
Herpestinae sp. C	×	
Herpestinae sp. D	×	
Herpestinae sp. E	×	
Hyaenidae		
Percrocuta australis	×	
Hyaenictis preforfex		×
Euryboas sp. nov.	×	
Hyaena abronia	×	×
Hyaenidae sp. B	×	
Hyaenidae sp. E		×

	Quartzose Sand Member	Pelletal Phosphorite Member
CARNIVORA (*cont.*)		
Felidae		
Machairodus sp.	×	
Homotherium sp.	?	×
Felis sp. (small)	×	
Felis aff. *issiodorensis*	×	×
Felis obscura		×
Dinofelis diastemata	×	×
Carnivora (possibly Lutrinae) gen. & sp. indet.	×	
PINNIPEDIA		
Phocidae		
Prionodelphis capensis	×	×
PROBOSCIDEA		
Gomphotheriidae		
Gen. & sp. indet.	×	×
Elephantidae		
Mammuthus subplanifrons	×	?
HYRACOIDEA		
Procavia cf. *antiqua*	×	?
PERISSODACTYLA		
Equidae		
Hipparion sp. A	×	
Hipparion sp. B	×	
Hipparion namaquense		×
Rhinocerotidae		
Ceratotherium praecox	×	?
ARTIODACTYLA		
Tayassuidae		
Gen. & sp. indet.		×
Suidae		
Nyanzachoerus sp(p).	×	×
Hippopotamidae		
Hippopotamus sp.		×
Giraffidae		
Sivatherium sp.	×	×
Giraffa sp.	×	×
Bobidae		
Tragelaphus aff. *angasi*	×	×
Mesembriportax acrae	×	×
Bovini gen. & sp. indet.	×	×
Reduncini sp. A		×
Reduncini sp. B		×
Alcelaphini sp. A		×
Alcelaphini sp. B		×
Raphicerus sp.	×	×
Gazella aff. *vanhoepeni*		×
?Ovibovini gen. & sp. indet.	×	
LAGOMORPHA		
Gen. & sp. indet.	×	×

	Quartzose Sand Member	Pelletal Phosphorite Member
RODENTIA		
Bathyergidae		
Bathyergus sp.	×	×
Cryptomys sp.	×	
Hystricidae		
Gen. & sp. indet.	×	
Muscardinidae		
Graphiurus sp.	×	
Cricetidae/Muridae		
Aethomys sp. A	×	
Aethomys sp. B	×	
Mus sp. A	×	
Mus sp. B	×	
Rhabdomys sp.	×	
Otomyinae gen. & sp. nov.	×	
Mystromys sp. A	×	
Mystromys cf. *darti*	×	
Mystromys cf. *hausleitneri*	×	
Desmodillus sp.	×	
Dendromus sp.	×	
Steatomys sp.	×	
Rodentia gen. & spp. indet.		×
CETACEA		
Gen. & spp. indet.	×	×

By far the best represented species is the seal, *Prionodelphis capensis* (Hendey & Repenning 1972). At the time that it was described, the species assemblage was already unusually large for a fossil phocid and since then many new specimens have been collected. *P. capensis* is evidently the best represented fossil phocid in the world. New material includes several nearly complete skulls (Fig. 6), parts of many more and hundreds of postcranial bones. Most of the material is from the Pelletal Phosphorite Member, the newest and best specimens having come from bed 3aN.

In view of the environments of deposition in the Varswater Formation, other aquatic carnivores are surprisingly rare. Only one specimen belonging to the otter, *Enhydriodon africanus*, is known, although the assemblage does include one unidentified carnivore which might also have been an otter (Hendey 1974*a*).

Until recently Canidae were known only on the basis of a few isolated teeth belonging to a small species and, as with the primate, there had been a growing doubt about identification. This doubt was dispelled by the discovery of a skull and associated postcranial bones belonging to the species. The skull has characters which indicate that the animal concerned was a fox (*Vulpes* sp.). It is known only from the Pelletal Phosphorite Member.

Another of the carnivores from this member, the bear, *Agriotherium africanum* (Hendey 1972*b*), remains one of the rarer elements in the fauna, although some additional postcranial bones were found recently.

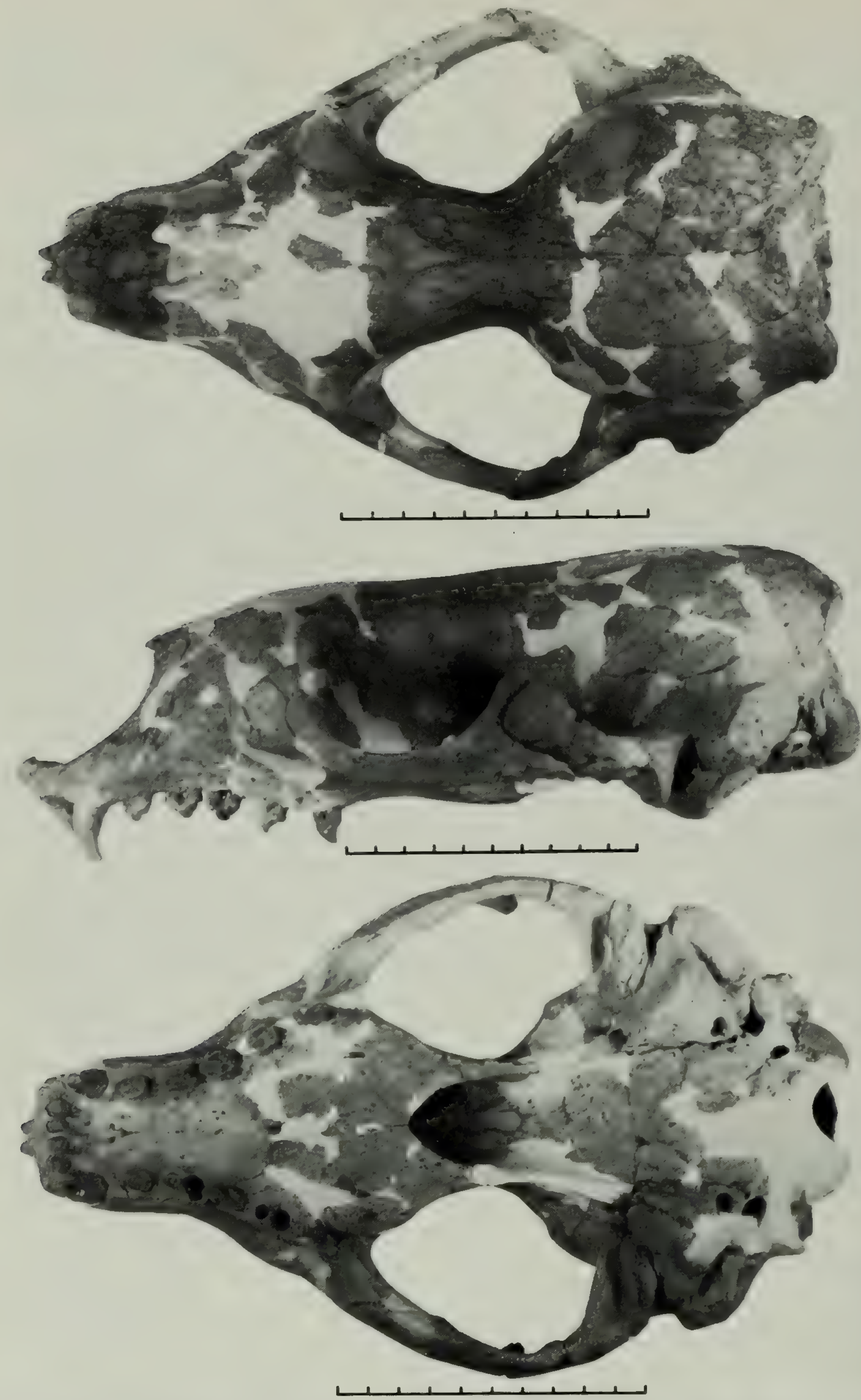

Fig. 6. Dorsal, lateral and ventral views of a skull of the seal, *Prionodelphis capensis* (SAM–PQ–L 31976) from bed 3aN, Pelletal Phosphorite Member, 'E' Quarry. Scale in centimetres.

Agriotherium was an unexpected addition to the 'E' Quarry fauna, being the first African record of the subfamily to which it belongs. Another similarly 'exotic' species was recently tentatively identified, this time a procyonid. The Procyonidae were widely distributed in Eurasia and North America during the late Tertiary, but have not previously been recorded from Africa. The Langebaanweg procyonid, if that is indeed what it is, may prove to be an enduring problem since it is poorly represented, with the only specimens having come from an area now covered by a mine dump. The specimens in question are fragments of the skull of an immature individual and parts of the hindfoot of an adult.

The Mustelidae include another of the new records for the site and this species is as exotic as the *Agriotherium* and ?procyonid in terms of the known distribution of its closest relatives. The new species is a giant form whose size approaches that of *Megalictis*, from the North American Miocene, which is the largest of all known mustelids. It belongs to a group of wolverine-like carnivores which includes *Megalictis* and which has previously been recorded only in Eurasia and North America. The presence in Africa of a member of this group is in a sense even more unexpected than the presence of the bear and ?procyonid since, unlike them, the giant wolverines are not recorded from southern Asia, which is the Eurasian region with the greatest faunal resemblances to Africa.

The giant wolverine and ?procyonid, which are both from the Quartzose Sand Member, join the list of Langebaanian species that belong to groups with an essentially Eurasiatic (and North American) record (Hendey 1974*a*: 61).

Apart from the otter, or otters, and the giant wolverine, the only other mustelid known from 'E' Quarry is a small, poorly represented species of *Mellivora* (Hendey 1974*a*), one additional specimen of which was recently collected from the Pelletal Phosphorite Member.

The Viverridae is the most diverse of the carnivore families known from the Varswater Formation. Previously only one civet (*Viverra leakeyi*) had been recorded, but new material indicates that there is at least one other species as well. The available civet material is problematical largely because it is so fragmentary. A large number of new specimens belonging to smaller viverrids have been discovered. Most of the material belongs to herpestines, but a small genet is also represented. When the herpestines were first studied (Hendey 1974*a*) only two species were recognized (*Herpestes* spp. A and B) and they are now the most commonly represented viverrids in the 'E' Quarry assemblage. The new material includes a few specimens which apparently belong to three additional species (Hendey 1974*b*: 157).

The most common of the larger terrestrial carnivores from the site are hyaenas, which now include one additional record, an apparently new species of *Euryboas*. The more advanced species of this genus were the long-legged and sharp-toothed 'hunting hyaenas' which occurred in Africa and southern Europe early in the Pleistocene (Hendey 1975). Four hyaena species had previously been recorded, namely, *Percrocuta australis*, *Hyaena abronia*, hyaenid species B and

Hyaenictis preforfex, while a fifth, hyaenid species E, was tentatively identified (Hendey 1974*a*). The status of the latter remains unresolved. Additional specimens, readily identifiable with *P. australis*, *H. abronia* and Species B, have been discovered, but *H. preforfex* is still only known from the remains of a single, aged individual. A detailed study of the hyaenid material now available is warranted. *H. abronia*, the best represented of the species, may prove particularly useful in resolving the problem of whether or not the Quartzose Sand and Pelletal Phosphorite Members are substantially different in age (*vide infra*).

The Felidae also include a recent new record, a small wildcat-sized species from the Quartzose Sand Member. Although specimens in addition to those already described have been discovered, only the false sabretooth, *Dinofelis diastemata*, is reasonably well represented.

Proboscideans

The Varswater Formation has yielded relatively few proboscidean specimens and those that have been found are generally fragmentary. The only exception is the incomplete skeleton of an elephant from the East Stream exposures of the Quartzose Sand Member (Maglio & Hendey 1970; Hendey 1974*a*: 349). Remains of an unidentified gomphothere occur more commonly than those of the elephant, *Mammuthus subplanifrons*.

Perissodactyls

Only one rhinoceros, *Ceratotherium praecox*, is known from the Varswater Formation (Hooijer 1972). It is perhaps the most commonly represented of the larger mammals from the Quartzose Sand Member, but only a few fragmentary specimens from the Pelletal Phosphorite Member may belong to this species.

The situation in respect of the Equidae is more complex. The material from the Quartzose Sand Member is here regarded as belonging to two species of *Hipparion*, an opinion rejected by Hooijer (in preparation). A few specimens thought to be from the Pelletal Phosphorite Member were excluded from Table 4 because of uncertainties about their provenance. Otherwise the only significant specimen from this member is an incomplete lower dentition from the uppermost level of the deposits in the bed 3aN area. Hooijer (in preparation) has referred it to *Hipparion namaquense* Haughton, 1932. It is notable in being the only record of this species in the Langebaanweg area. Also no other specimens from the same horizon have yet been positively identified.

The Equidae, perhaps more than any other group represented in the various fossil occurrences near Langebaanweg, are potentially important in resolving the problems of relative age and stratigraphic relationships of the deposits in which they occur. For example, although the Gravel Member in 'E' Quarry has produced few useful terrestrial vertebrate fossils, one interesting exception is an incomplete equid tooth, which, together with two teeth from the same horizon in 'C' Quarry, is tentatively identified with the Miocene species, *Hipparion primigenium*. Hooijer (in preparation) also rejects this identification, but if the material does indeed represent a Miocene species, it must have been reworked from the underlying Saldanha Formation. This formation would therefore be younger than 12,5 m.y. B.P., since before this date *Hipparion* was not present in Africa, or elsewhere in the Old World (Hooijer 1975).

The Baard's Quarry assemblage includes both *Hipparion* and *Equus*, the latter indicating that at least part of the fauna is younger than that from the Varswater Formation. The *Hipparion* material from Baard's has recently proved to be as controversial as that from 'E' Quarry, but the assemblage is here regarded as being comprised of two species, the more commonly represented being distinct from the 'E' Quarry hipparions. Earlier it had been indicated that only one *Hipparion* was represented in the Langebaanweg occurrences (Hendey 1972*a*; 1974*a*), but this is now discounted. The various issues relating to the Langebaanweg equids should eventually be resolved satisfactorily.

Artiodactyls

Perhaps the most unexpected of the recent new records from 'E' Quarry is that of a peccary. Previously the species concerned had been regarded as a miniature pig (Hendey 1974*a*: 47), but additional material from bed 3aN led to the revised identification being suggested by both A. W. Gentry (British Museum (Natural History)) and H. B. S. Cooke (Dalhousie University) (pers. comm.). This is the first African record of the family Tayassuidae and it is also the most recent Old World occurrence. The nearest peccary record in both a geographic and temporal sense is the Miocene *Pecarichoerus orientalis* from the Siwalik Hills of India (Colbert 1933). The Langebaanweg peccary, which is one of the smallest ever recorded, was the subject of a recent preliminary study (Hendey in press).

Nyanzachoerus is the only pig which occurs in the Varswater Formation and it is known from most of the fossiliferous exposures of the Quartzose Sand Member, having been particularly common in the East Stream area. The species from this member is remarkably well represented, the available assemblage being larger than those of previously described members of this genus. Recently *Nyanzachoerus* was recorded from the Pelletal Phosphorite Member for the first time. The specimen concerned, a fragmented and incomplete skull, differs in some respects from the Quartzose Sand Member specimens and probably represents a second species. Although not yet studied in detail, the Quartzose Sand Member *Nyanzachoerus* has already proved useful in the relative dating of the deposits (Hendey 1973), and the Pelletal Phosphorite Member species promises to be equally useful in this respect (see p. 244).

The apparent absence of hippopotamus from the 'E' Quarry fauna has previously given rise to comment, since the depositional environments of the Varswater Formation were such that this animal might have been expected to occur quite commonly (Hendey 1974*a*: 48). A few fragmentary hippo remains were found for the first time during 1975 in the bed 3aN exposures of the Pelletal Phosphorite Member. The fact that hippos are rare in this member and that they are still not recorded from the extensively sampled Quartzose Sand Member has yet to be satisfactorily explained.

The 'E' Quarry Giraffidae are fairly well represented by elements of the postcranial skeleton, but cranial material is rare and invariably fragmented and incomplete. Some of the best giraffid specimens, belonging to both *Sivatherium* and *Giraffa*, have come from bed 3aN. The material is being studied by J. M. Harris (Kenya National Museum).

One additional bovid species, a reduncine, was recently recorded from 'E' Quarry. Curiously, Bovidae are not as well represented at this site in terms of numbers of individuals as they are at some of the Pleistocene fossil occurrences in the region. In addition, there are relatively few species recorded from the Quartzose Sand Member, which is otherwise remarkable for the diversity of species represented. On the other hand, certain deposits tend to include individuals of particular species in numbers which are disproportionately high in terms of their bovid assemblages as a whole. For example, the boselaphine, *Mesembriportax acrae* (Gentry 1974), is by far the most commonly occurring bovid in the Quartzose Sand Member, while in bed 3aS it is alcelaphines which are abundant. At least some of the Quartzose Sand Member boselaphine remains are believed to have accumulated sub-aerially, indicating that this species was an inhabitant of the area now exposed in the mine. Gentry (1974) suggested that the boselaphine was an open woodland species and this sort of habitat may well have existed in the immediate vicinity of the old estuary. The situation in respect of the Pelletal Phosphorite alcelaphines was probably quite different. Many, and perhaps all of the specimens were apparently washed to their final resting-places by the river and their carcasses may have originated upstream where the river crossed open plains, the probable preferred habitat of the alcelaphines.

Other mammals

Other terrestrial mammals recorded from the Varswater Formation include a pangolin, an aardvark, a dassie (hyrax) and a porcupine. All are rare. Cetacea are more common, but are represented mainly by undiagnostic postcranial bones. Both whales and dolphins occur, remains of the latter having been found for the first time during 1975.

The porcupine is known only from a fragmented skull of a large and unidentified species which is currently being studied by Judy M. Maguire (Bernard Price Institute for Palaeontological Research). This specimen was found in the Quartzose Sand Member shortly after publication of a comment on the supposed absence of porcupines from the Varswater Formation (Hendey 1974*a*: 42).

The dassie, *Procavia* cf. *antiqua*, was originally identified on the basis of very fragmentary specimens, but more and better material is now available. The most complete specimens are from easterly exposures of the Quartzose Sand Member.

The aardvark is amongst the most poorly represented of the 'E' Quarry mammals and until recently the same applied to the pangolin. The situation in respect of the latter has been slightly improved by the discovery of an incomplete skeleton, including parts of the skull, much of the tail and parts of all four limbs.

FLORA

Prior to the exposure of the peat bed the only botanical remains recovered from the 'E' Quarry exposures of the Varswater Formation were some fossil root fragments from the Quartzose Sand Member. A series of samples from the peat bed submitted to the Institute for Environmental Sciences at the University of the Orange Free State included one which was pollen-rich. Approximately 92 per cent of the sporomorphae belonged to one unidentified taxon (E. M. van Zinderen Bakker pers. comm. to A. J. Tankard). This may represent a locally abundant marsh plant. Interestingly, both tree and grass pollens were identified and this lends support to the earlier suggestion that these vegetation types must have been present in the area at the time that the deposits were laid down (Hendey 1973).

During 1975 two boreholes were sunk from the floor of the mine into deposits underlying the Varswater Formation. They intersected two peat horizons which are evidently part of the Miocene Saldanha Formation. These peats contain both visible and microscopic plant remains.

DATING

A Pliocene age for the Varswater Formation, with an inferred chronometric date of 4–5 m.y. B.P., is still accepted, but there have been new developments concerning the dating of fossils from the Gravel Member and the age difference between the Quartzose Sand and Pelletal Phosphorite Members.

The Gravel Member is composed largely of an abraded and fragmented phosphatic rock which is known to contain bone fragments and which is undoubtedly pre-Pliocene in age. The rock, and other deposits with which it may have been associated, was eroded during the early stages of the Pliocene marine transgression (Fig. 2). The possibility that some fossils might have been reworked from the deposits truncated by the transgression has been recognized, but was not substantiated until a study of the Gravel Member Selachii by P. A. Hulley revealed that some specimens are evidently of pre-Pliocene age. The derived fossils may also include the few isolated *Hipparion* teeth referred to earlier (see p. 240). The derived pre-Pliocene element in the Gravel Member fossil assemblage is likely to make up but a small part of the assemblage as a whole.

Still unresolved is the question of the time taken for the Varswater Formation to accumulate. There were clearly intervals of time between the deposition of fossils at different levels in the succession, but so far as is known the only one which may have been of sufficient duration to be palaeontologically significant was that between the deposition of the Quartzose Sand and Pelletal Phosphorite Members. The original opinion that the faunas of the two members were broadly contemporaneous (Hendey 1970*b*) was based on the fact that they do have species in common and on the belief that differences between them were due simply to a general dissimilarity in the modes and environments of deposition of the fossils.

On the other hand, the Pelletal Phosphorite Member does postdate the Quartzose Sand Member and it has been recognized that the time factor may have been significant enough to be reflected in the characteristics of individual species represented in the succession and to have influenced the overall composition of the two faunas. Previous studies on species common to the two faunas have provided no conclusive evidence of significant evolutionary changes. For example, the suggestion that the Pelletal Phosphorite *Viverra leakeyi* might be a more advanced variety of the same species from the Quartzose Sand Member (Hendey 1974*a*: 81) has still not been substantiated. In this and other instances comparisons have been complicated mainly by inadequacies in the available material.

The most important indication to date that the two faunas may be separated by a substantial period in time came with the discovery of the first *Nyanzachoerus* specimen from the Pelletal Phosphorite Member. The new specimen is in certain respects more advanced than the Quartzose Sand Member *Nyanzachoerus* and if there was an ancestor/descendant relationship between the two forms, their difference in age may be of the order of several hundred thousand years. Although comparisons with *Nyanzachoerus* species recorded elsewhere are 'complicated by the uniqueness of the 'E' Quarry forms', indications are that the one from the Pelletal Phosphorite is unlikely to be less than 4 m.y. old, while that from the Quartzose Sand dates back probably no more than 5 m.y.

Now that more material from the Pelletal Phosphorite Member is becoming available, the potential for meaningful comparisons between the two main faunas from 'E' Quarry is greatly increased.

Relative dating of the 'E' Quarry fossils and deposits has been based on comparisons of some mammals with their counterparts at various localities in East Africa. The fact that this dating is neither very secure nor very precise is due to the small number of species which have been appropriate for such comparisons. It is increasingly apparent that the Langebaanweg fauna is a good deal more unique than had hitherto been supposed and although individual species do have much in common with their contemporaries further north, they are not always identical. If the fauna does indeed include local endemics, and also perhaps late survivors of lineages which were already extinct elsewhere, the faunal dating of the occurrences will become complicated and less satisfactory.

CONCLUSIONS

The 'E' Quarry fossil occurrences, which are the most important in the Langebaanweg area, are significant for a variety of reasons. There are very few recorded sites in southern Africa which have yielded vertebrate fossils of comparable age and the assemblages from such sites are minuscule by comparison. Consequently the only substantial information on the nature of the subcontinental vertebrate fauna of 4–5 million years ago is derived from the 'E' Quarry record. The nearest important fossil occurrences which are broadly contemporaneous are in East Africa, about 4 500 kilometres away (e.g. Vogel River Series, Lower Kaiso Formation, Mursi Formation of the Omo Group, Kanapoi/Lothagam and Kubi Algi at East Rudolf). However, not even these occurrences have produced assemblages so large and so diverse as that from 'E' Quarry. Elsewhere in Africa the Pliocene fossil record is either poor or nonexistent, so Langebaanweg is an especially important source of information on the animal life of this epoch not only in a local sense, but for Africa as a whole. It has the additional merit of being the only important Pliocene occurrence on the continent where both marine and terrestrial faunas are represented.

Certain of the 'E' Quarry species assemblages are already impressively large and, since collecting is continuing, they are still growing. The preservation of specimens is generally very good, all skeletal elements are represented (and collected) and unequivocal associations of cranial and postcranial material are not uncommon. It should therefore ultimately prove possible to provide comprehensive definitions of many species and this may well assist in resolving identification problems in the smaller assemblages from other African sites.

The species diversity is remarkable by any standards and as a result the fauna as a whole will be better known than those of many other sites where important elements may be lacking (e.g. vertebrate microfauna, birds, aquatic species).

The 'E' Quarry fauna, like many others in southern Africa, has so far been dated only in a relative sense and in this respect it is more problematical than many from East Africa. However, the Langebaanweg occurrences are amongst the very few of any importance in southern Africa where generally acceptable geological dating is also possible.

Perhaps the biggest drawback of the site lies with its situation at the southern continental extremity, far from the main focus of African late Cenozoic palaeontological investigation (i.e. East Africa). On the other hand, this may ultimately invest it with a particular interest since, as the contemporary East African fauna becomes better known, similarities and differences of zoogeographic significance may emerge.

ACKNOWLEDGEMENTS

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6. SYSTEMATIC papers must conform with the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. n., sp. n., comb. n., syn. n., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family **Nuculanidae**

Nuculana (*Lembulus*) *bicuspidata* (Gould, 1845)

Figs 14–15A

Nucula (*Leda*) *bicuspidata* Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (figs 8a–b).
Nucula largillierti Philippi, 1861: 87
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:
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dash, not comma, separates consecutive numbers

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In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33.51S, 25.39E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and of date.

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(a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '. . . the Figure depicting *C. namacolus* . . .'
'. . . in *C. namacolus* (Fig. 10) . . .'

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e.g. Du Toit but A. L. du Toit
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(c) Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

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Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as
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Q. B. HENDEY

THE PLIOCENE FOSSIL OCCURRENCES IN 'E' QUARRY, LANGEBAANWEG, SOUTH AFRICA

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KOHN, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon.—*Ann. Mag. nat. Hist.* (13) **2**: 309–320.

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THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* **4**: 269–270. Jena: Fischer.—*Denkschr. med.-naturw. Ges. Jena* **16**: 269–270.

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NOTES ON THE ADDUCTOR JAW MUSCULATURE OF *VENJUKOVIA*, A PRIMITIVE ANOMODONT THERAPSID FROM THE PERMIAN OF THE U.S.S.R.

By

HERBERT R. BARGHUSEN

Cape Town Kaapstad

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(With 4 figures)

[*MS accepted 9 March 1976*]

ABSTRACT

The primitive anomodont *Venjukovia*, from Zone II of the Russian Permian, has been thought to bridge the morphological gap between dinocephalians and dicynodonts. Much of the pattern of adductor jaw musculature in *Venjukovia* conforms closely to that found in dicynodonts and is thereby consistent with the hypothesis that these are closely related forms. The most important similarity is the probable presence in *Venjukovia* of a distinctive lateral division of the external adductor. The presence of this division is a derived character previously known only in dicynodonts. However, as far as can be determined, similarities between *Venjukovia* and dinocephalians only involve joint possession of a primitive therapsid arrangement of various other parts of the jaw musculature. Therefore, the muscle pattern does not provide evidence of a closer relationship with dinocephalians than with other primitive therapsid groups. Moreover, in contrast to primitive dinocephalians (brithopodids), *Venjukovia* lacks an extensive area of origin of the external adductor from the dorsal surface of the temporal roof. The absence of this specialized area of origin suggests (tentatively) that *Venjukovia* retained the primitive therapsid condition of the temporal roof and that the lines leading to *Venjukovia* and dicynodonts on the one hand and to dinocephalians on the other diverged before the primitive dinocephalian condition was achieved.

CONTENTS

	PAGE
Introduction	249
Material	250
Adductor jaw musculature . . .	252
Conclusions	258
Acknowledgements	259
References	259
Abbreviations	259

INTRODUCTION

The Russian anomodont *Venjukovia* has long attracted attention because it shows structural resemblances to tapinocephalid dinocephalians on the one hand (Efremov 1940) and to dicynodonts on the other (Watson 1942, 1948). Efremov noted general resemblances between *Venjukovia* and tapinocephalids in the structure of the teeth, face and palate. Watson agreed but also noted that the lower jaw of *Venjukovia* shows many features which are, in essence, identical with those in dicynodonts. Romer (1956) regarded *Venjukovia* as seeming to bridge the morphological gap between dinocephalians

Ann. S. Afr. Mus. **69** (10), 1976: 249–260, 4 figs.

and dicynodonts. It is not the purpose of this paper to extensively analyse the phylogenetic position of *Venjukovia*; the issues involved are complex and demand a thorough phylogenetic analysis of therapsids in general which is the subject of a paper in preparation. However, the present study, which involves a partial reconstruction of adductor jaw musculature in *Venjukovia*, has obvious potential for defining character states useful in such an analysis. In addition, some general but very tentative conclusions concerning the possible relationships between *Venjukovia*, dinocephalians and dicynodonts can be advanced based on a comparison of their patterns of adductor jaw musculature. Accordingly, such comparisons will be made in so far as it is possible to do so in this paper.

A rationale for jaw muscle reconstruction in synapsid reptiles and a reconstruction of this musculature (based on a reptilian model) in the pelycosaur *Dimetrodon* has already been provided (Barghusen 1973). The evaluation of direct evidence of muscle attachment as well as the arguments concerning the distribution of individual jaw muscles presented for *Dimetrodon* also apply to the reconstructions made here. For this reason, the reader is referred to Barghusen (1973) for clarification of the issues involved. In addition, by virtue of the phylogenetic position of *Dimetrodon* within the pelycosaur family from which therapsids were derived, the pattern of jaw musculature which it shows constitutes the pattern primitive to the evolution of this musculature in therapsid reptiles. Therefore, comparisons of the reconstructed musculature in *Venjukovia* will also be made with that of *Dimetrodon* exemplifying the pre-therapsid arrangement from which the musculature of *Venjukovia* was derived.

MATERIAL

The reconstruction of adductor jaw musculature presented here for *Venjukovia* is based on information gained from a skull of *V. prima* (PIN 2793/1) and three lower jaws of *V. invisa* (PIN 157/1111, 157/1112, 157/5) housed in the Palaeontological Institute, U.S.S.R. Academy of Sciences, Moscow. The skull is exceptionally well-preserved except posteriorly where much of the bone forming the posterior margin of the lateral temporal fenestra, the posterior root of the zygomatic arch, and the occiput has flaked from the matrix. Nevertheless, the bone which is present, and impressions of bone in the matrix, clearly indicate that the outlines of the lateral temporal fenestra, temporal fossa, zygomatic arch, and the position of the quadrate correspond to that shown in Figures 1A and 1C. Matrix has not been cleared from the temporal fossae or the orbits. For this reason it is impossible to estimate the area of origin of m. adductor mandibulae internus pseudotemporalis, m. adductor posterior, and, if present, m. adductor mandibulae internus pterygoideus anterior. Consequently, these muscles will not be considered in this reconstruction. However, the medial surface of the lower jaw (Fig. 1D) has not departed sufficiently from that of *Dimetrodon* to suggest that the general areas

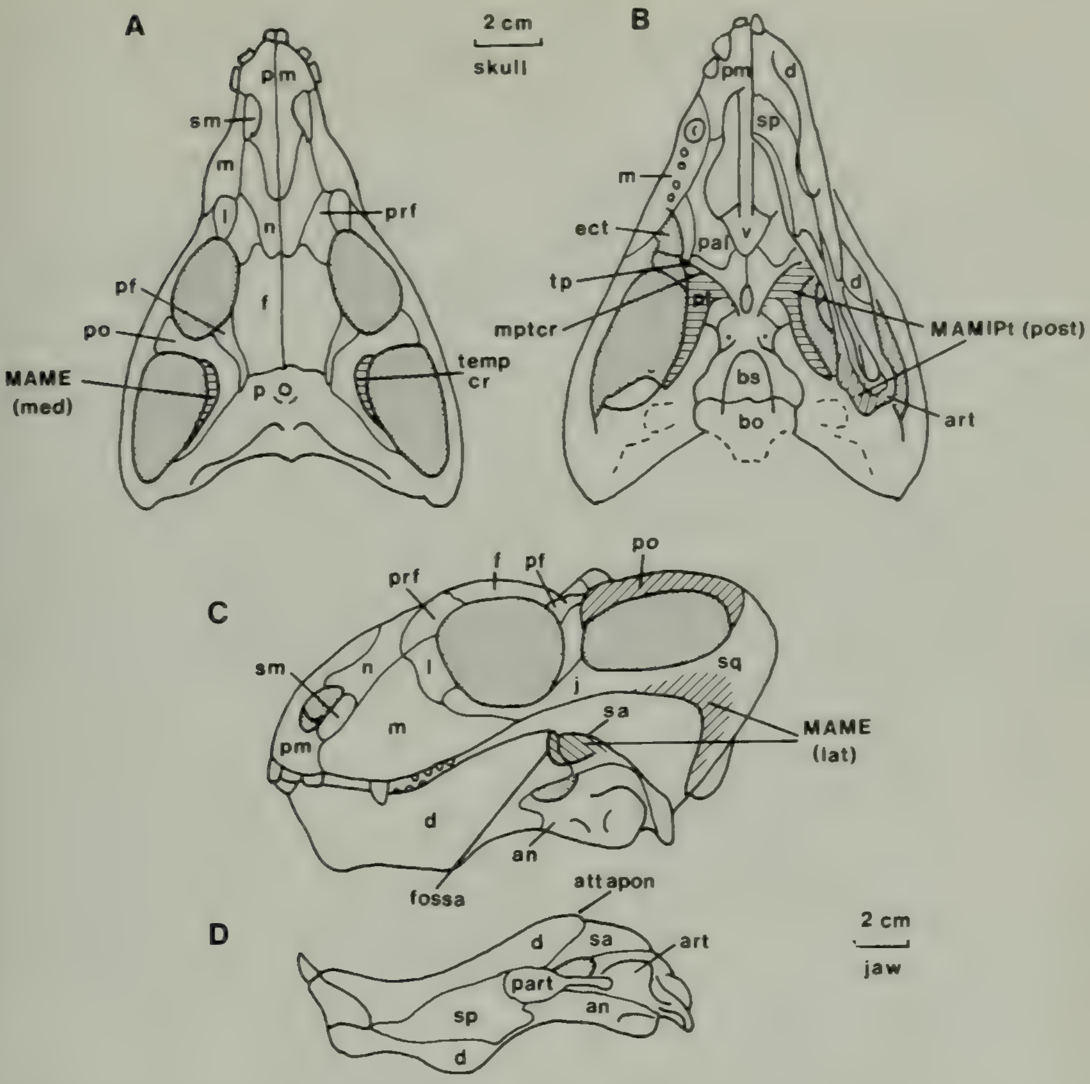

Fig. 1. Reconstruction of the skull and lower jaw of *Venjukovia*.
A. Dorsal view of skull. B. Ventral view of skull with left lower jaw in place. C. Lateral view of skull and lower jaw. D. Medial view of lower jaw. The areas of origin and insertion of the external adductor and posterior pterygoideus jaw musculature are indicated by parallel lines. The outline of the posterior margin of the skull and the position of the quadrate were determined from bone impressions in the matrix. (Skull reconstructed from PIN 2793/1; lower jaw reconstructed from PIN 157/1111, 157/1112, 157/5.)

of insertion of these muscles were significantly different from those in *Dimetrodon*.

The reconstruction of brithopodid jaw musculature is also based on specimens housed in the Palaeontological Institute, Moscow. These include an exceptionally well-preserved skull and lower jaw of *Titanophoneus potens* (PIN 157/1). Details of the temporal fossa were also gained from *Notosyodon gusevi* (PIN 2505/1).

Much of the information upon which the reconstruction of musculature in *Lystrosaurus* is based was collected in 1965 at Yale University from an acid-prepared skull (SAM–4325). Unfortunately this skull was subsequently destroyed in transit. More recently, information has also been gained from acid-prepared material examined while the author visited the South African Museum, Cape Town. This material included a skull and lower jaw of *L. declivis* (Nat. Mus. C 403).

ADDUCTOR JAW MUSCULATURE

M. ADDUCTOR MANDIBULAE EXTERNUS

The temporal region of *Venjukovia* exhibits the posterodorsal enlargement of both the lateral temporal fenestra and temporal fossa which is characteristic of most therapsids as opposed to sphenacodontid pelycosaurs (cf. Figs 2A, C). In dorsal view (Fig. 1A) the temporal fossa is broadly exposed due to the extensive but as yet incomplete reduction in the width of the temporal roof. The degree of reduction is comparable to that seen in some dicynodonts (cf. *Emydops*, Crompton & Hotton 1967, Fig. 1B) but not as extensive as that found, for example, in *Lystrosaurus* (Fig. 3A). The presence of a temporal crest (Fig. 1A, temp cr) in *Venjukovia* provides direct evidence that the external adductor took origin from the lateral face of that part of the postorbital forming

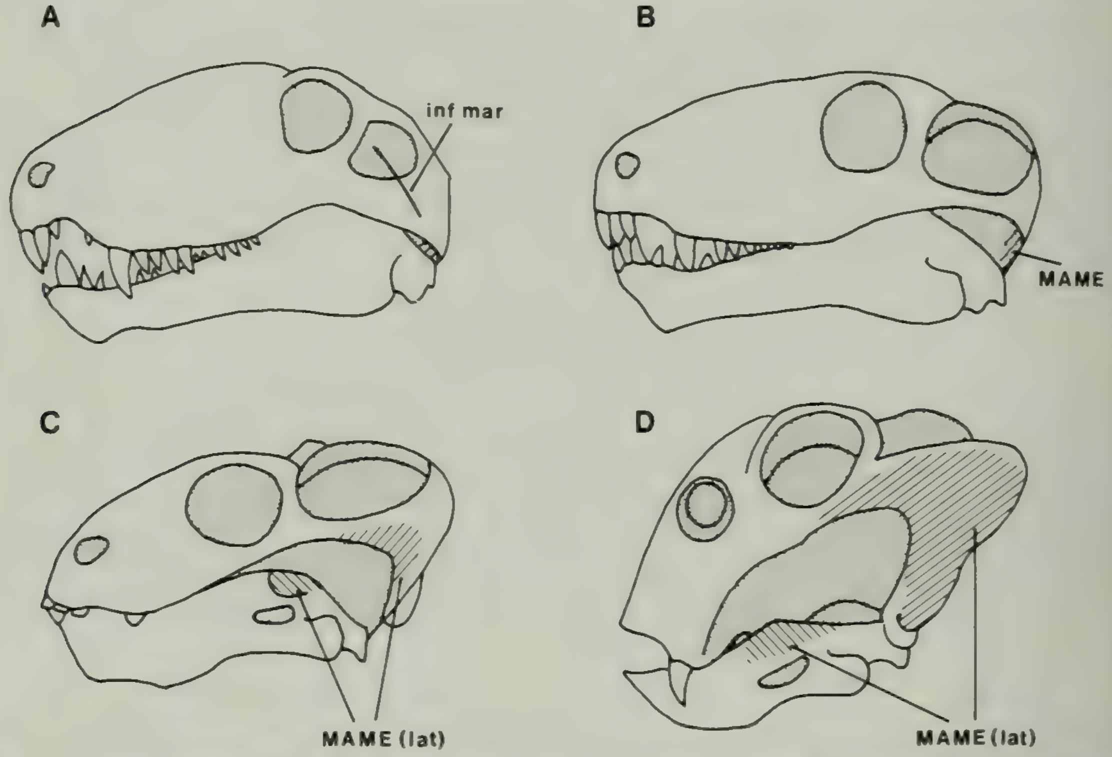

Fig. 2. Lateral views of the skull and lower jaw of Dimetrodon, A, hypothetical condition, B, *Venjukovia*, C, and *Lystrosaurus*, D, forming a morphological series which illustrates stages in the development of the lateral division of the external adductor jaw musculature characteristic of dicynodonts. In A the zygomatic arch is positioned close to the adducted lower jaw. In B the zygomatic arch is dorsally displaced creating an access route for that part of the external adductor originating from the anterior face of the quadratojugal and quadrate to invade the lateral surface of the squamosal. In C and D the arch is further displaced and the invasion, creating the lateral division of the external adductor, has taken place; in addition, an area of insertion for the lateral division is established on the dorsolateral surface of the lower jaw. (A after Romer and Price.)

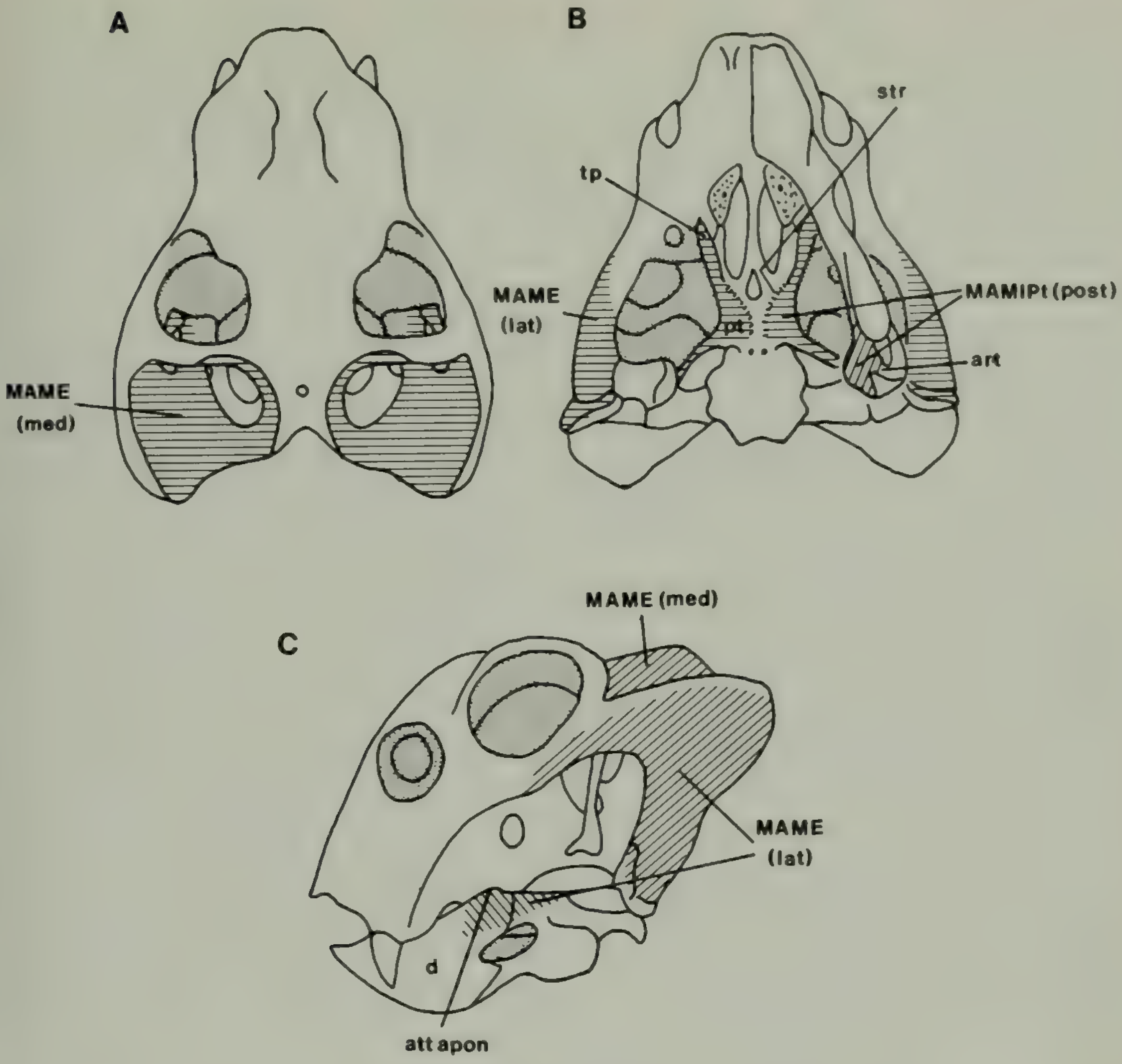

Fig. 3. The skull and lower jaw of *Lystrosaurus*.
A. Dorsal view of skull. B. Ventral view of skull with left lower jaw in place. C. Lateral view of skull and lower jaw. The areas of origin and insertion of the external adductor and posterior pterygoideus muscles are indicated by parallel lines.

the lateral margin of the temporal roof. The establishment of muscle origin here probably represents an invasion of muscle attachment from the anterior face of that part of the squamosal forming the posterior wall of the temporal fossa. This condition, which is a distinct departure from that found in sphenacodontids, was probably common among primitive therapsids as it is also found in gorgonopsids, *Biarmosuchus*, and *Eotitanosuchus* (personal observations). The extent of this muscle attachment on the postorbital also approaches that seen in dicynodonts (e.g. *Lystrosaurus*, Fig. 3A; also see Crompton & Hotton 1967; Cluver 1975). *Venjukovia*, however, does not achieve the specialized condition seen in brithopodids, the most primitive known dinocephalians. In brithopodids, the external adductor took extensive origin from the dorsal surface of the temporal roof (Fig. 4A; also see Watson 1948; Olson 1962; Boonstra 1963; Barghusen 1973). The condition in brithopodids contrasts sharply with that found in other primitive therapsids (i.e. gorgonopsids, *Eotitanosuchus*, *Biarmosuchus*, and ictidorhinids) as well as in *Venjukovia*. All these animals retain the sphenacodontid arrangement, in which no adductor jaw musculature attaches to the dorsal surface of the temporal roof. In contrast to more primitive dinocephalians, many tapinocephalid dinocephalians (e.g. *Moschops*) reverted back to the primitive therapsid and sphenacodontid arrangement in the sense that the attachment of the external adductor to the dorsal surface of the temporal roof was eliminated. Evidence strongly suggests that this reversal in tapinocephalids was related to the development of head-butting behaviour in these animals (Barghusen 1975). Conceivably a reversal may also have taken place in the ancestry of *Venjukovia*. However, *Venjukovia* does not exhibit any of the specializations for use of the dorsal surface of the head in butting which are displayed by tapinocephalids and which, if present in *Venjukovia*, would suggest tapinocephalid relationships. At the moment it seems more likely, therefore, that the condition manifested by *Venjukovia* is a retention of the primitive therapsid and pelycosaur condition as there are no obvious functional reasons to suggest that the absence of muscle attachment to the dorsal surface of the temporal roof was secondarily derived. If so, *Venjukovia* reflects a morphological stage, with regard to the attachment of part of the adductor musculature, resembling that which must have been antecedent to the stage reached by the most primitive known dinocephalians. Such a conclusion appears to be implicit in Boonstra's (1963) remarks to the effect that when the dinocephalian and dicynodont lines diverged, the intertemporal skull table was broad and the origin of the adductor muscles showed a fairly primitive condition. This conclusion runs counter to suggestions (Efremov 1940) that *Venjukovia* was derived from tapinocephalids.

Preparation of the temporal fossa is not complete in the skull of *Venjukovia*. However, there are reasons to believe that the undersurface of much of the retained portion of the temporal roof served for the attachment of the external adductor. This is expected from the distribution of the attachment of this muscle in living reptiles. In addition, a depression on the undersurface of the roof indicates that this was the case in *Dimetrodon* (see Barghusen 1973) and a similar scar or depression has been found in all therapsids examined in which the temporal region was sufficiently prepared and which showed a degree of development of the temporal roof similar to that of *Venjukovia*. These therapsids include *Titanophoneus* (see Orlov 1958, fig. 21) and *Notosyodon* among the dinocephalians and *Leontocephalus* (see Kemp 1969, fig. 5) among the gorgonopsids. This evidence clearly suggests that such an arrangement of muscle attachment was present prior to and during the evolution of those therapsids that did not completely eliminate the temporal roof. It is also expected (Barghusen 1973) that the dorsal and ventrolateral parts of the posterior wall of the temporal fossa, including the squamosal and quadrate, served as an area of origin of the external adductor muscle in *Venjukovia*. The squamosal portion of this area of attachment to the posterior wall of the fossa would have served

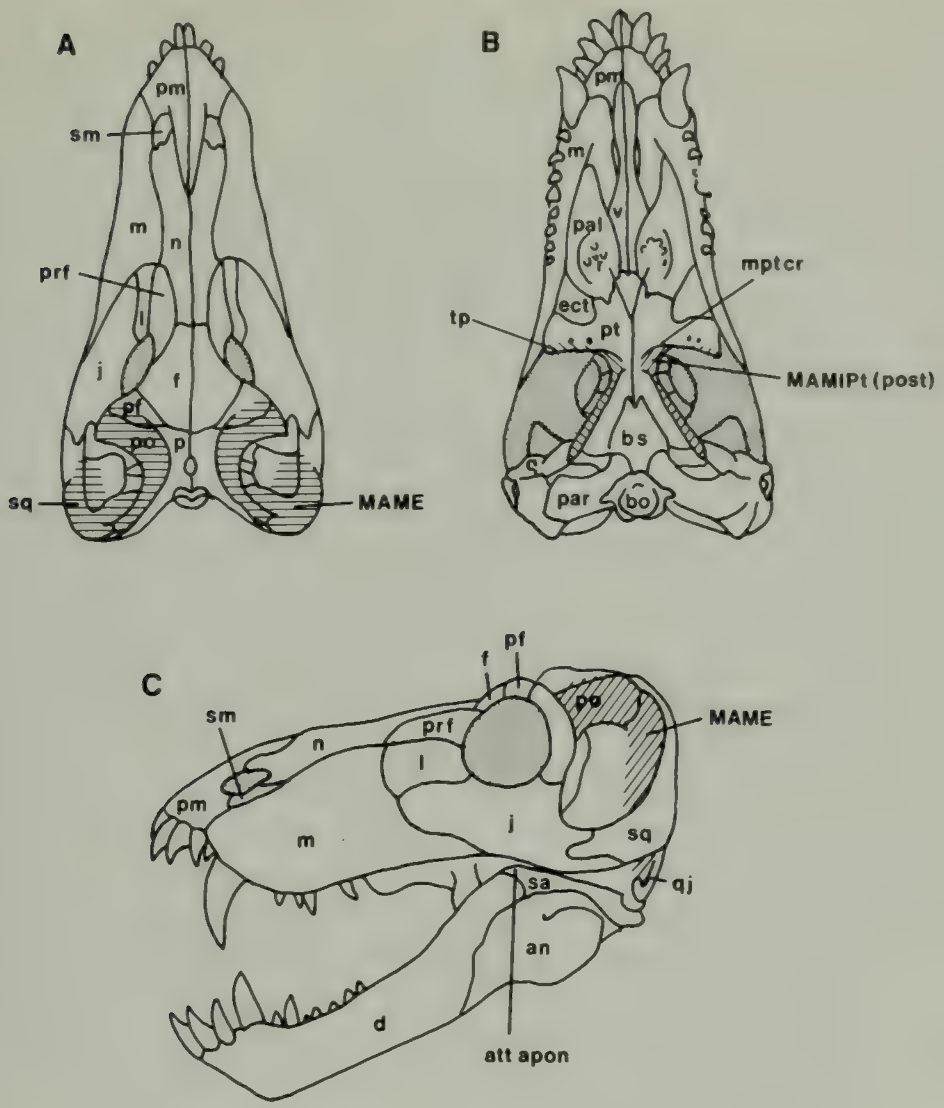

Fig. 4. The skull and lower jaw of *Titanophoneus*.
A. Dorsal view of skull. B. Ventral view of skull. C. Lateral view of skull and lower jaw. The areas of origin of the external adductor and posterior pterygoideus muscles are indicated by parallel lines. (Outlines after Orlov.)

as the original site from which the invasion of muscle attachment onto the lateral surface of the postorbital in therapsids, including *Venjukovia*, took place.

The posterodorsal tip of the dentary, forming the apex of the coronoid eminence in *Venjukovia*, marks the probable site of attachment of a bodenaponeurosis (Fig. 1D, att apon) serving for the insertion of much of that part of the external adductor described above. This function for the coronoid eminence is indicated by comparisons with living reptiles (Barghusen 1973) and is consistent with direct evidence of tendon attachment in *Dimetrodon* (Barghusen 1968) and theriodont therapsids. A similar insertion would also have been present in all dinocephalians (Fig. 4C, att apon) and, as Cluver (1975) has recently pointed out, in dicynodonts, in which the posterodorsal tip of the dentary marks a site of tendinous attachment (Fig. 3C, att apon) identical in position to that in *Venjukovia.*

By far the most important question concerning the external adductor in *Venjukovia* is whether or not a lateral division was present comparable to that found in dicynodonts (Figs 2D, 3B, C). The external adductor jaw musculature independently established an extensive area of attachment on the zygomatic arch and exposed lateral surface of the lower jaw at least twice and probably three times in therapsid history. This definitely occurred in cynodonts (Barghusen 1968) and dicynodonts (Watson 1948; Crompton & Hotton 1967; Cluver 1975) and probably occurred in gorgonopsids (Barghusen 1968; Kemp 1969). In each group the manner in which this muscular modification occurred is highly distinctive. In cynodonts a laterally bowed zygomatic arch created a channel through which developing masseter musculature descended from the temporal fossa to insert on the lateral surface of the dentary; subsequent events led to the establishment of muscular origin on the entire zygomatic arch. An invasion also occurred in gorgonopsids but in this case the muscle attachments were confined to the lateral surface of the angular and the posterior root of the zygomatic arch. In dicynodants, a channel was created for the invasion of musculature from the confines of the temporal fossa through the dorsal displacement of the zygomatic arch relative to the dorsal surface of the lower jaw (Crompton & Hotton 1967). This invasion resulted in a newly added lateral division of the external adductor originating from the arch and expanded lateral surface of the squamosal and inserting on a distinctive lateral shelf of the dentary (Crompton & Hotton 1967; also see Figs 3B–C). This muscular development is a dicynodont hallmark, as is the developing masseter muscle for cynodonts.

Despite the limitations of incomplete preservation posteriorly, the morphology of *Venjukovia* indicates that this animal closely conforms to, and may reflect, an initial stage in the development of the condition seen in dicynodonts. The zygomatic arch is dorsally displaced relative to the jaw articulation. This created the necessary condition whereby external adductor musculature originating on the ventrolateral part of the posterior wall of the temporal fossa (the quadratojugal and quadrate as reconstructed in *Dimetrodon* (Barghusen 1973)) had free access to invade the lateral surface of the squamosal by a route passing inferior to the level of the zygomatic arch (Fig. 2). It is also apparent (Fig. 2) that the zygomatic arch of *Venjukovia* and dicynodonts was dorsally displaced to the level of the inferior margin (Fig. 2A, inf mar) of the attachment of the external adductor to the inner surface of the cheek as reconstructed in *Dimetrodon* on the basis of stretch capabilities of muscle (see Barghusen 1968). This suggests that much of the length of the inferior and medial surfaces of the arch could have served for the origin of musculature with sufficient fibre length to allow for a substantial gape (also see Watson's 1948 discussion of gape in dicynodonts). Finally, this displacement removes the zygomatic arch from immediate proximity to the lateral surface of the lower jaw which, thereby, becomes a potential site of muscle insertion.

The extent of invasion of muscle attachment onto the lateral surface of the squamosal is impossible to determine in *Venjukovia* due to insufficient preservation of the posterior root of the zygomatic arch. However, the presence of a fossa (Fig. 1C, fossa) excavated into the lateral surface of the surangular and most posterior part of the dentary, as a departure from the primitive therapsid condition, strongly suggests that such invasion did take place. The fossa indicates the incipient development of muscle attachment to the dorsolateral surface of the jaw corresponding to the insertion of the lateral division of the external adductor in dicynodonts (Fig. 3C); the insertion has merely expanded anteriorly in dicynodonts to include more of the dentary. The fossa thus indicates the presence of a laterally placed muscle whose area of origin may well have included the lateral surface of the squamosal. If so, the impression of the squamosal left on the matrix suggests that the posterior root of the zygomatic arch was shaped as in Figure 1C and capable of supporting an area of origin from its lateral surface as is illustrated.

M. ADDUCTOR MANDIBULAE INTERNUS PTERYGOIDEUS (POSTERIOR)

The area of origin of the posterior pterygoid muscle in *Venjukovia* is clearly very similar to that reconstructed in *Dimetrodon* (Barghusen 1973). A boss on the distal end of the transverse process of the pterygoid as well as indications of a medial pterygoid crest (Fig. 1B, m pt cr) provide direct evidence of tendinous attachment in the manner of sphenacodontids, theriodonts, and brithopodids (Fig. 4B), as well as many living reptiles. The ventral surface of the quadrate ramus of the pterygoid is also expected to have served as an area of origin for this muscle mass (Fig. 1B, MAMIPt (post)). The major difference in area of origin of the posterior pterygoid muscle between *Venjukovia*, on the one hand, and *Dimetrodon* and brithopodids, on the other, is that the transverse process is less massive and projects anterolaterally in *Venjukovia* (cf. Figs 1B, 4B). The anterolateral projection approaches (but by no means achieves) the condition in dicynodonts, in which the transverse process has lost its role in bracing and controlling the movements of the lower jaw and projects almost straight forward (Fig. 3B, tp). In this regard, *Venjukovia* resembles a morphological stage which was probably antecedent to the condition in dicynodonts.

It is generally assumed that the transverse process of the pterygoid is either reduced (Romer 1956) or entirely eliminated (Watson 1948; Crompton & Hotton 1967) in dicynodonts. It appears, however, that this structure is merely redirected forward and in many cases is well developed. The structure labelled as the transverse process in Figure 3B has the same general topographic relationships to the subtemporal fossa and the ectopterygoid (when the latter is present) as does the structure which is clearly the transverse process in *Venjukovia*. Moreover, direct evidence in one acid-prepared specimen (SAM–4325) of *Lystrosaurus* indicates that the relationship to the posterior pterygoid muscle is also the same. The ventral surface of the distal portion of the process is slightly rugose and striated, suggesting tendon attachment. In addition, a line of parallel striations (Fig. 3B, str) extends posteromedially from the ventral edge of the anteriorly directed process to terminate near the level of the basipterygoid joint. The position of this line corresponds to that of the medial pterygoid crest and also provides direct evidence of probable tendon attachment.

The area of insertion of the posterior pterygoid muscle in *Venjukovia* (Fig. 1B) is expected to have included the ventromedial surface of the articular and probably the anteromedial face of the retroarticular process. This reconstruction contrasts with many made in the past in which it was assumed that pterygoideus musculature ran beneath the jaw to insert on the lateral surface of the main body of the angular medial and posterior to the reflected lamina. This has been thought to have been the case in sphenacodontid pelycosaurs and in therapsids in general (see Barghusen 1968, 1973; Crompton & Hotton 1967; Watson 1948). The muscle involved has been given various names and reconstructed with a number of different areas of origin; however, it is the posterior pterygoid muscle as reconstructed by Barghusen (1973). While an insertion on the lateral surface of the angular appears to be valid for sphenacodontids, its validity is questionable in most therapsids. As pointed out by Allin (1975), the very close relationship between the reflected lamina and the lateral surface of the main body of the angular in the vast majority of therapsids, including brithopodids, *Venjukovia*, and dicynodonts, argues against the intervention of musculature between these structures. The confinement of musculature within such a narrow space would cause functional inefficiency since the amount of muscle is necessarily very small and, as Allin remarks, the muscle 'would be unable to shorten without bulging against its skeletal confines as well as constricting off its own blood supply, although an associated venous plexus might provide volumetric compensation'. It may be added that if a venous plexus were present in the space between the lamina and main body of the angular, the amount of musculature present would have been negligible. It is more reasonable, as persuasively argued by Allin, to regard this space as housing an air-filled chamber existing as a tympanic or pharyngeal diverticulum and functioning in sound reception.

CONCLUSIONS

The pattern of adductor jaw musculature reconstructed for *Venjukovia* suggests that this animal is closely related to dicynodonts—perhaps more closely related to dicynodonts than to any other known therapsid group. A close relationship is indicated by: 1. the probable presence of a similar lateral division of the external adductor in both groups in contrast to the condition in other therapsids; and 2. the fact that the structure of the area of origin of the posterior pterygoid in *Venjukovia* is consistent with the structure postulated for a theoretical morphological stage transitional to the dicynodont condition. The muscular morphology of *Venjukovia* contrasts with that of primitive dinocephalians in that there is no specialized origin of the external adductor from the dorsal surface of the temporal roof in *Venjukovia*. Unless a reversal (i.e. secondary elimination of this area of origin) is postulated, animals which would be classified as dinocephalians were not involved in the ancestry of *Venjukovia*. At the moment, there is no evidence which suggests that such a reversal took place. The therapsid ancestry of *Venjukovia* is, the author believes, an open question.

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ABBREVIATIONS

an	angular
art	articular
att apon	attachment of the bodenaponeurosis
bo	basioccipital

bs	basisphenoid
d	dentary
ect	ectopterygoid
f	frontal
inf mar	inferior margin of the origin of the external adductor from the inner surface of the cheek
j	jugal
l	lacrimal
m	maxilla
MAME	external adductor muscle
MAME (lat)	lateral division of the external adductor muscle
MAME (med)	medial division of the external adductor muscle
MAMIPt (post)	posterior pterygoid muscle
m pt cr	medial pterygoid crest
n	nasal
p	parietal
pal	palatine
par	paroccipital process
part	prearticular
pf	postfrontal
pm	premaxilla
po	postorbital
prf	prefrontal
pt	pterygoid
q	quadrate
sa	surangular
sm	septomaxilla
sp	splenial
sq	squamosal
str	striations
temp cr	temporal crest
tp	transverse process of the pterygoid
v	vomer
Nat. Mus.	National Museum, Bloemfontein, South Africa.
PIN	Palaeontological Institute, Moscow, U.S.S.R.
SAM	South African Museum, Cape Town, South Africa.

6. SYSTEMATIC papers must conform with the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae
Nuculana (*Lembulus*) *bicuspidata* (Gould, 1845)
Figs 14–15A

Nucula (*Leda*) *bicuspidata* Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (figs 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:
comma separates author's name and year
semicolon separates more than one reference by the same author
full stop separates references by different authors
figures of plates are enclosed in parentheses to distinguish them from text-figures
dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33.51S, 25.39E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers, date and geographical positions.

7. SPECIAL HOUSE RULES

Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '. . . the Figure depicting *C. namacolus* . . .'; '. . . in *C. namacolus* (Fig. 10) . . .'

(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene

(c) Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as
'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

HERBERT R. BARGHUSEN

NOTES ON THE ADDUCTOR JAW MUSCULATURE OF *VENJUKOVIA*, A PRIMITIVE ANOMODONT THERAPSID FROM THE PERMIAN OF THE U.S.S.R.

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For books give title in italics, edition, volume number, place of publication, publisher.

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Examples (note capitalization and punctuation)

Bullough, W. S. 1960. *Practical invertebrate anatomy*. 2nd ed. London: Macmillan.

Fischer, P.-H. 1948. Données sur la résistance et de le vitalité des mollusques.—*J. Conch., Paris* **88**: 100–140.

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(*continued inside back cover*)

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ISOPODAN AND TANAIDACEAN CRUSTACEA FROM THE ST PAUL AND AMSTERDAM ISLANDS, SOUTHERN INDIAN OCEAN

By

BRIAN KENSLEY

Cape Town Kaapstad

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ISOPODAN AND TANAIDACEAN CRUSTACEA FROM THE ST PAUL AND AMSTERDAM ISLANDS, SOUTHERN INDIAN OCEAN

By

Brian Kensley

South African Museum, Cape Town

(With 26 figures)

[*MS accepted 26 February 1976*]

ABSTRACT

A collection of land and marine Isopoda and Tanaidacea from the St Paul and Amsterdam Islands, southern Indian Ocean, is dealt with. Three species of tanaids and thirty-four species of isopods are discussed. Of these, seven new species are described, viz. *Eisothistos crateris*, *Panathura amstelodami*, *Cymodocella sapmeri*, *Munnogonium subtilis*, *Coulmannia unicornis*, *Echinomunna uroventralis*, and *Ianisera trepidus*. The latter species belongs to the new genus *Ianisera*, while a species of *Janira*, viz. *J. angusta* Barnard, is transferred to the new genus *Ianiroides*. The isopod fauna is analysed into zoogeographical components. It is shown that there is a strong endemic fauna (27%), as well as a South American/Antarctic/Subantarctic and a widespread component, but by far the largest component (35%) is that group common to the islands and South Africa (mostly the west coast of South Africa). It is concluded that the isopod fauna of the St Paul and Amsterdam Islands falls into the cold-temperate faunal category with strong affinities to the fauna of South Africa.

CONTENTS

	PAGE
Introduction	261
Review of published work	262
Species list	263
Station list	268
Systematic discussion	271
Zoogeographical discussion	318
Acknowledgements	321
References	321

INTRODUCTION

During 1971–2, a research programme centred on the St Paul and Amsterdam Islands was sponsored by Terres Australes et Antarctiques, with the logistic support of the Société Anonyme de Pêche Maritime et de Ravitaillement (S.A.P.M.E.R.). As part of this programme, J. Beurois of the Station Marine d'Endoume et Centre Oceanographie, Marseille, made extensive collections of invertebrates from these islands, both intertidally and subtidally. The marine and the few terrestrial isopods collected were submitted to the author for identification. The following is an account of the species found, with a discussion of their zoogeographical implications. Most of the type specimens are deposited in the Paris Museum of Natural History. A few paratypes are deposited in the South African Museum, and are designated 'SAM'.

Ann. S. Afr. Mus. **69** (11), 1976: 261–323, 26 figs.

REVIEW OF PUBLISHED WORK ON ISOPODA FROM THE ST PAUL AND AMSTERDAM ISLANDS

The St Paul and Amsterdam Islands, situated at 38.43S, 77.32E and 37.55S, 77.40E respectively (see fig. 1), almost midway in the southern Indian Ocean, and just north of the Subtropical Convergence, have been visited by biologists at infrequent intervals. The Austrian frigate *Novara* called at the islands during its circumnavigation of the earth in 1857–9. A preliminary report on the isopods by C. Heller was published in 1861, while the full report appeared in 1865. This dealt with five species of isopods and one tanaid: *Idotea nitida*, *Cleantis granulosa*, *Porcellio paulensis*, *Sphaeroma perforata*, *Cirolana rugicauda* and *Tanais gracilis*.

Brocchi (1877) reported on a collection of isopods made by Velain and d'Lisle during the French mission sent to observe the passage of Venus. Nine species were dealt with, viz. *Idotea nitida*, *Porcellio paulensis*, *Sphaeroma perforata*, *Sphaeroma tuberculata*, *Cymodoce picta*, *Cirolana rugicauda*, *Rocinela major* and *Cymothoa gadorum*. This material, unfortunately, cannot be located and must be presumed lost.

The German South-Polar Expedition of 1901–3 visited the islands on the *Gauss*. Vanhöffen (1914) reported on the marine isopods, listing seven species and one tanaid: *Cirolana rugicauda*, *Cycloidura perforata*, *Dynamenella brunnea*, *Jaeropsis paulensis*, *Antias hispidus*, *Antias marmoratus*, *Janira* sp. and *Tanais gracilis*. Budde-Lund (1906) dealt with the land isopods of this expedition and mentions *Deto armata* from St Paul. Finally, André (1932) lists three species, viz. *Paridotea ungulata*, *Cycloidura perforata* and *Porcellio paulensis*.

To date, the total number of isopods from the St Paul and Amsterdam Islands numbers 16 species, 4 of these being of uncertain identity. The present collection includes 35 species, bringing the total number of isopods to 44, this more-than-doubling of the number being a reflection of the very thorough collecting carried out by J. Beurois.

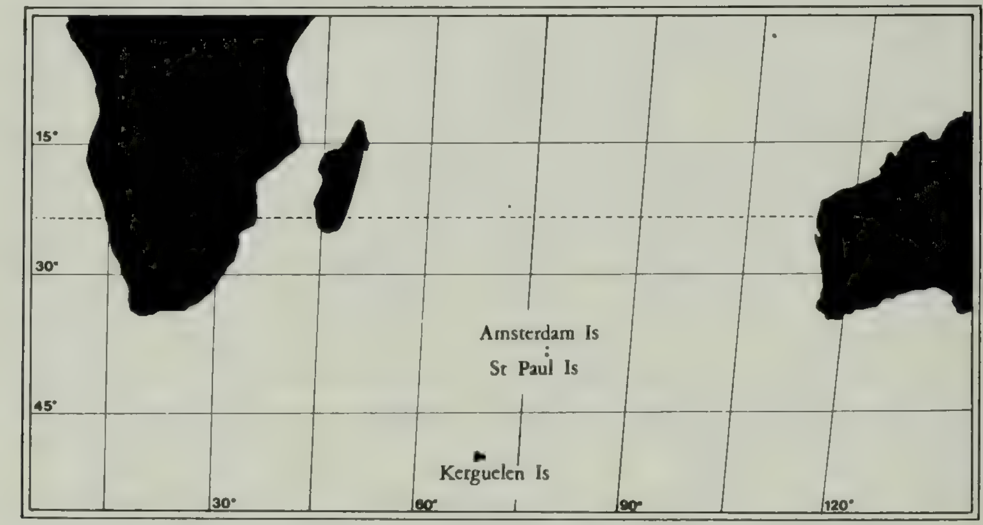

Fig. 1. Map showing position of the St Paul and Amsterdam Islands.

SPECIES LIST

In the following list, the species are arranged in the order in which they are dealt with in the systematic section.

*—not dealt with in systematic section.

	St Paul and Amsterdam habitat and depth distribution				General distribution		
SPECIES	Littoral	Upper infralittoral	Sublittoral	Endemic	South Africa	South America Antarctic	Other
TANAIDACEA							
Anatanais gracilis (Heller)	—	among kelp roots, stones	under stones and sponges, 25–50 m		Lüderitz to Durban	—	Ceylon
Leptochelia barnardi Brown	—	among kelp roots	among stones and algae		Table Bay False Bay	—	—
Leptochelia savignyi (Kröyer)	—	among kelp roots	among stones and algae		Lüderitz to Moçambique	—	North and and South Atlantic Mediterranean Indo-Pacific
ISOPODA							
* *Cleantis granulosa* Heller	under gravel and stones				—	Argentina Tierra del Fuego	—
Idotea metallica Bosc	—		on buoy cable		Cape to Moçambique	Straits of Magellan Patagonia Antarctic	Greenland, Tristan Nova Scotia
Paridotea nitida (Heller)	—	among kelp roots, stones, algae, 3–4 m	among algae and sponges 25–30 m	+	—	—	—
Paridotea reticulata Barnard	—	on *Macrocystis* 'leaves' 0–5 m			Lüderitz to False Bay	—	—

	St Paul and Amsterdam habitat and depth distribution			General distribution			
SPECIES	Littoral	Upper infralittoral	Sublittoral	Endemic	South Africa	South America Antarctic	Other
Eisothistos crateris sp. nov.	—	from rock scrapings, on sponges, bryozoa	—	+	—	—	—
Panathura amstelodami sp. nov.	—	among kelp roots	from rock, algae, sponges, 50–80 m	+	—	—	—
Panathura serricauda (Barnard)	—	among kelp roots, algae	—		Lüderitz to False Bay	—	—
Cirolana rugicauda Heller	—	among kelp, algae, stones, sponges in organic debris, 0,6 m	—		Port Nolloth St Helena Bay	—	—
* *Cymodocea picta* Brocchi							
Cymodocella sapmeri sp. nov.	amongst algae	among kelp roots, algae, 1–4 m	among algae, sponges, bryozoa, 60 m	+	—	—	—
Dynamenella brunnea Vanhöffen	amongst algae, stones	among kelp roots, stones, sponges, 1–4 m	—	+	—	—	—
Dynamenella dioxus Barnard	—	among kelp roots 3–4 m	from sponges, algae, 25–60 m		Lüderitz to False Bay	—	—
Parisocladus perforatus (H. M. Edwards)	intertidal pools among stones, algae	amongst algae, in black sediment 3 m	—		Rocky Point, S.W.A., to East London	—	—
* *Spheroma tuberculata* Brocchi	—	—	—				
Limnoria quadripunctata Holthuis	—	in kelp roots	in red algae 30 m			Chile	North Sea California

* *Cymothoa gadorum* Brocchi						
Lironeca raynaudii (H. M. Edwards) . . .	on gill cover of *Latris lineata*			Table Bay Durban	—	New Zealand, Japan, Tasmania, Australia
Aega antillensis Schiödte & Meinert	on *Thyrsites atun*			Natal	—	Japan, West Indies
Aega monilis Barnard . . .	—	—	among sponges, corals, 60–70 m	Table Bay, East London	— —	— —
* *Rocinela major* Brocchi .						
Stenetrium crassimanus Barnard	—	—	among algae, corals, sponges	False Bay Natal	—	—
Stenetrium saldanha Barnard .	—	—	among algae, sponges, 50–90 m	Saldanha Bay False Bay Still Bay	—	—
Antias dimorphus Menzies . .	—	among kelp, algae	amongst organic debris, algae, sponges, from coarse sand, 50–80 m	—	Chile Kerguelen	—
Antias hispidus Vanhöffen . .	—	among kelp, algae, sponges	among algae, sponges, in black sediment, 50–60 m	—	Auckland Is. Falkland Is. Antarctic	—
Antias hofsteni Nordenstam .	—	—	among algae, sponges, stones, 45–100 m	—	South Georgia	—
Caecianiropsis ectiformis (Vanhöffen)	—	—	scrapings from boulder	—	Kerguelen Is.	—
Ianiroides angusta (Barnard) .	—	—	among algae, sponges, 25 m	False Bay	—	—

	St Paul and Amsterdam habitat and depth distribution			General distribution			
SPECIES	Littoral	Upper infralittoral	Sublittoral	Endemic	South Africa	South America Antarctic	Other
Ianisera trepidus sp. nov.	—	—	among sponges, bryozoa, corals, 30–100 m	+	—	—	—
Janira capensis Barnard	—	among kelp roots on *Macrocystis* 0,6 m	among stones, algae, sponges, bryozoa		Lüderitz to False Bay	—	—
Ianiropsis palpalis Barnard	among algae, stones, intertidal pools	among algae, sponges, kelp 0,6 m	among stones, sponges, algae, bryozoa, on gorgonian, 40–120 m		Lüderitz to East London	—	—
Jaeropsis beuroisi Kensley	—	among kelp roots 0,3 m	among corals, bryozoa, sponges, 25–80 m	+	—	—	—
Jaeropsis paulensis Vanhöffen	—	among kelp roots, stones, organic debris	on sponges, bryozoa		—	Gough Is.	—
Munnogonium subtilis sp. nov.	—	—	50–60 m	+	—	—	—
Coulmannia unicornis sp. nov.	—	—	80–100 m	+	—	—	—
Echinomunna uroventralis sp. nov.	—	—	on bryozoa, corals, sponges	+	—	—	—
Munna nana Nordenstam	—	on kelp roots, among *Ulva* 0,6 m	among algae, corals, bryozoa, sponges, 50–120 m			Chile Falkland Is.	—

Munna sp.	—	—	on coral, sponges, 80–100 m	—	—	—
Deto echinata Guérin . . .	upper and mid-littoral crevices, under stones	—	—	Rocky Point, S.W.A., to Knysna	—	—
Porcellio scaber Latreille . .	feeding on kelp washed ashore		—	Cape	Tristan da Cunha, St Helena Is.	—

STATION LIST

AMSTERDAM ISLAND (AMS)

Station No.	*Date*	*Depth (metres)*	*Locality and ecological data*
a1	10.2.1971	upper infralittoral	north coast; obtained from scraping 400 cm² amongst abundant algae
a2	10.2.1971	upper infralittoral	north coast; obtained from scraping 400 cm² amongst *Ulva* and *Splachnidium*
a3	10.2.1971	upper infralittoral	north coast; obtained from scraping 400 cm² amongst *Splachnidium*
a4	11.2.1971	upper infralittoral	north coast; among rock crevices and kelp holdfasts
a5	11.2.1971	upper infralittoral	north coast; in *Laminaria* holdfasts
a6	11.2.1971	upper infralittoral	north coast, amongst algae
a7	11.2.1971	upper infralittoral	north coast, under stones, and in clean sediment
a8	27.2.1971	upper infralittoral	north coast, under stones
a9	27.2.1971	midlittoral	north coast among boulders
a10	27.2.1971	between midlittoral and sublittoral	north coast, in wet sediment
b1	12.2.1971	littoral	north—north-east coast; amongst algae and sponges
b2/1a	12.2.1971	midlittoral	north—north-east coast; amongst small molluscs and algae
b2/1b	12.2.1971	lower midlittoral	north—north-east coast
b2/2	12.2.1971	midlittoral	north—north-east coast amongst *Porphyra* and *Splachnidium*
b3	12.2.1971	upper infralittoral	north—north-east coast under stones
c1	14.2.1971	midlittoral	east coast; scrapings from algal growth on wall
c2	14.2.1971	midlittoral	east coast; scrapings from wall
c3	14.2.1971	upper infralittoral	east coast; scrapings from cavity
3	9.2.1971		north coast; algae from lobster pot
5a	19.2.1971		north coast, from *Macrocystis* holdfast washed ashore
5b	19.2.1971		north coast, from *Macrocystis* holdfast washed ashore
6a	19.2.1971		north coast, from *Laminaria* holdfast
6b	19.2.1971		north coast, from *Laminaria* holdfast
8	22.2.1971	upper infralittoral	north coast, under stones
	23.2.1971	low tide	north coast, natural tide-pool
10	23.2.1971	0,5	north coast, under stones
11	24.2.1971	40–50	south-east coast from lobster pot
12	27.2.1971	midlittoral	north coast, under stones
14	9.3.1971	upper midlittoral	north coast, in tide-pools
15	9.3.1971	midlittoral	north coast
16	9.3.1971	upper sublittoral	north coast, amongst red algae
23	5.12.1971		on *Macrocystis* fronds
28	5.12.1971	120	north-east coast, from coralligenous bottom, with bryozoa, sponges, and corals
39	11.12.1971	80–100	north-east coast, from coralligenous bottom
41a	13.12.1971	80–100	north-east coast from antipatharian epifauna
41b	13.12.1971	80–100	north-east coast, from encrusting fauna of stones, sponges, bryozoans, etc.
44	14.12.1971	80–100	north-east coast, from antipatharian epifauna

Station No.	*Date*	*Depth (metres)*	*Locality and ecological data*
48	16.12.1971	80–100	north-east coast from bryozoans encrusting antipatharian trunk
60	2.1.1972	80–100	south-east coast from gorgonacian *Acanthogorgia*
64a	3.1.1972	80	south-east coast epifauna from cable submerged for one year
64b	3.1.1972		south-east coast, from buoy and 3-metre floating cable
73	6.1.1972	80–100	north-east coast, from coralligenous bottom
74	8.1.1972		north-east coast, from encrusting fauna of stone
78	9.1.1972	25	from buoy cable
83	9.1.1972		south-east coast, from encrusting fauna of stones
94	13.1.1972	60–100	north-east coast, from bryozoans encrusting antipatharian trunk
96	13.1.1972	80–100	north-east and south coasts, washed from variety of coralligenous organisms
100	14.1.1972	0–5	north-east coast, on *Macrocystis* fronds
101	14.1.1972	80–100	east coast, from epifauna of antipatharian
103	15.1.1972	80–100	north-east coast, from epifauna of antipatharian
111	16.1.1972	80–100	north-east coast, from encrusting fauna of stones
119	20.1.1972	80	north-east coast, from epifauna of bryozoan
132	22.1.1972	80–100	east coast, from epifauna of gorgonacian *Acanthogorgia*
133	23.1.1972	80–100	north coast, from sponges and corals
142a	25.1.1972	50	south-west coast, from epifauna of bryozoans and sponges
142b	25.1.1972	50	south-west coast, from epifauna of algae and sponges
143	25.1.1972	25–30	south-west coast, from amongst red algae and sponges
147	25.1.1972	60	west coast, from amongst algae, corals, and sponges
148	25.1.1972	80	west coast, from sponge on antipatharian base
173	12.2.1972	50–60	north-east coast, from epifauna of antipatharian trunk
D1	6.12.1971	80–90	south-east of island
D7	2.1.1972	60–80	east coast
D12	23.2.1972	40–50	north coast
D9	23.1.1972	50–60	east coast
B9	17.12.1971	50	north-east coast

In the following stations, the date of collection is also the station number:

Date	*Depth (metres)*	*Locality and ecological data*
2.5.1969		east coast, from amongst alga *Pterocladia*
27.3.1970a	sublittoral	north coast, from crevices in rocks
27.3.1970b	sublittoral	north coast, from crevices in rocks
28.3.1970a	sublittoral	north coast, from crevices in rocks and under stones
28.3.1970b	sublittoral	north coast, from rocky wall and pools

Date	*Depth* (*metres*)	*Locality and ecological*
12.12.1970	70	on dead antipatharian trunk
16.1.1971	30	north-east coast, from *Macrocystis* holdfast
17.1.1971	30	east coast, from encrusting fauna of rock

Isopods from the following stations were all taken from the stomach and digestive tracts of the fish *Acantholatris monodactylus*, all taken with a line, from 2 to 3 metres depth, in February–March 1971:

P1, P2, P6, P7, P13a, P13b, P11, P16, P17, P23, P26, P27, P28, P29, P30, P31, P33, P34, P36, P37, P38, P39, P42, P44, P46, P47, P48, P49, P50.

Isopods from the following station were taken from the stomach contents of the rock lobster *Jasus paulensis*:

J11.

ST PAUL ISLAND

Station No.	*Date*	*Depth* (*metres*)	*Locality and ecological data*
3	19.12.1971	2–3	north edge of crater, from amongst sponges, bryozoans, and ascidians growing on submerged gill net
6a	19.12.1971	sublittoral	inside crater, amongst algae
6c	19.12.1971	sublittoral	inside crater, amongst *Ulva*
7a	20.12.1971	sublittoral	inside crater, amongst algae
7b	20.12.1971	sublittoral	inside crater, from under stones
8a	20.12.1971	mid- to sublittoral	inside crater, amongst stones and algae
8b	20.12.1971		inside crater, from black sediment between stones and algae
8c	20.12.1971		inside crater, amongst organic debris and green algae
14	21.12.1971	upper sublittoral	exterior of north jetty, amongst red algae
15	21.12.1971	littoral	exterior of north jetty, from amongst *Splachnidium rugosum*
16	21.12.1971	sublittoral	exterior of north jetty, on rocks
18	21.12.1971	sublittoral	inside crater, amongst encrusting algae, sponges, and ascidians
19	21.12.1971		from rock scrapings
20	21.12.1971		from rock scrapings
22a	22.12.1971	sublittoral	inside crater, amongst encrusting corals, bryozoa, and worm tubes on boulders
22b	22.12.1971	sublittoral	inside crater, amongst encrusting algae on boulders
22c	22.12.1971	sublittoral	inside crater, amongst encrusting ascidians, sponges and bryozoans
23	22.12.1971	sublittoral	amongst encrusting algae, sponges and bryozoans
23a	22.12.1971	sublittoral	amongst encrusting algae, sponges, and ascidians
24a	22.12.1971	upper sublittoral	from *Laminaria* holdfast
24b	22.12.1971	upper sublittoral	from *Laminaria* holdfast
26	23.12.1971	littoral	exterior of crater, east coast
27	23.12.1971	littoral	exterior of crater, east coast
28	23.12.1971	littoral	amongst algae exterior of crater, east coast
30a	23.12.1971	0,6	inside crater, from *Laminaria* holdfast
30b	23.12.1971	0,6	inside crater, from *Laminaria* holdfast
32	23.12.1971	0,6	inside crater, from *Macrocystis* fronds
35	26.12.1971	3,0	inside crater, amongst sponges, ascidians and algae

Station No.	*Date*	*Depth (metres)*	*Locality and ecological data*
59	28.1.1972		from stomach contents of fish *Thyrsites atun*
67	30.1.1972	80–100	south-east coast, amongst encrusting algae, bryozoans and ascidians
77a	2.2.1972		from *Macrocystis* holdfast
77b	2.2.1972		from *Macrocystis* holdfast
82	4.2.1972		on operculum of fish, *Latris lineata*
85	4.2.1972	60–70	north-east coast, from encrusting sponges, worm tubes, and corals
90	15.2.1972	sublittoral	inside crater, from encrusting sponges, bryozoans, ascidians, etc.
91	15.2.1972	sublittoral	inside crater, from encrusting worm tubes, and green algae
B7	24.12.1971	45	inside crater, from encrusting bryozoans, worm tubes and algae on stones
B19	27.1.1972	30	exterior of crater, amongst red algae and bryozoans
D3	30.1.1972	50–80	north-east coast, from coarse sandy bottom
D5a	30.1.1972	3–4	east coast, from *Laminaria* holdfast
D5b	30.1.1972	3–4	east coast, from *Laminaria* holdfast
D5c	30.1.1972	3–4	east coast, from red algae
D6	16.2.1972	40–50	north-east coast, from red algae, and bryozoans
D8	16.2.1972	40	north-east coast, from coarse sediment

In the following stations the date of collections is also the station number:

Date	*Depth (metres)*	*Locality and ecological data*
1970		exterior of crater, from *Macrocystis*
29.12.1970	25–30	exterior of crater, amongst sponges, ascidians and hydroids
1.1.1971		on floating buoy
3.1.1971		interior of crater, found in fishing boat
29.1.1971	80–100	exterior of crater, from submerged cable

SYSTEMATIC DISCUSSION

Order TANAIDACEA

Family **Tanaidae**

Anatanais gracilis (Heller)

Tanais gracilis Heller, 1865: 133, pl. 12 (fig. 3). Vanhöffen, 1914: 468, fig. 6a–g. Barnard, 1925*a*: 381; 1940: 489.

Previous records

Lüderitzbucht to Durban, St Paul and Amsterdam Islands, Ceylon.

Material

AMS	a4	1	St Paul	6c	1
	b3	1		7a	2
	11	1		7b	1
	74	1		8a	1 ovig. ♀ + 1
	142b	1		D5/c	1 ovig. ♀ + 1
				18	2
				20	3
				22b	1 ovig. ♀
				77a	2
				90	3
				93	2

Leptochelia barnardi Brown

Leptochelia barnardi Brown, 1957: 406, figs 4a–c, 5a.

Previous records

False Bay, Table Bay.

Material

AMS	a4	6	St Paul	90	1

Leptochelia savignyi (Kröyer)

Leptochelia savignyi: Brown, 1957: 404, fig. 5b (synonymy).

Previous records

Lüderitzbucht to Moçambique, north and south Atlantic, Mediterranean, Indo-Pacific.

Material

AMS	a4	7	St Paul	B7	1
				7b	1
				D5/c	1
				19	1
				90	2

Order ISOPODA

Suborder VALVIFERA

Family **Idoteidae**

Idotea metallica Bosc

Idotea metallica: Barnard, 1914: 203; 1940: 507. Schultz, 1969: 78, fig. 97.

Previous records

Wide-ranging, almost cosmopolitan: Cape, Moçambique, Natal, Tristan da Cunha, Greenland, Nova Scotia, Straits of Magellan.

Material

AMS	78	1 ovig. ♀

Genus *Paridotea* Stebbing

Heller (1861, 1865) and Brocchi (1877) in their lists of isopods from St Paul and Amsterdam Islands both include *Idotea nitida*. Hale (1924), André (1932), and Sheppard (1957) place *I. nitida* in the synonymy of *Paridotea ungulata* (Pallas). Examination of the idoteids from St Paul and Amsterdam Islands in the present collection, however, revealed two abundant species of *Paridotea*, neither being *P. ungulata*. Examination of Heller's type material, and comparison with *P. ungulata* from the Cape, make it clear that *P. nitida* is a valid species.

Paridotea nitida (Heller)

Fig. 2B, D, F

Idotaea nitida **Heller, 1861: 497.**
Idotea nitida **Heller, 1865: 131, pl. 12 (fig. 1). Brocchi, 1877: 97.**

Previous records

St Paul Island.

Material

AMS	2.5.69	1 ♂	5 ♀♀		St Paul	D5/b		1 ♀	
	a4	2 ♂♂	2 ♀♀			D5/c	3 ♂♂	4 ♀♀	
	a5		2 ♀♀			6c	2 ♂♂		1 ovig. ♀
	a6	16 ♂♂	24 ♀♀	17 juv.		7a	2 ♂♂		
	a7	2 ♂♂				14	26 ♂♂	21 ♀♀	
	a8	1 ♂	1 ♀			19	2 ♂♂		2 ovig. ♀♀
	C1	12 ♂♂	18 ♀♀			20		1 ♀	1 ovig. ♀
	C2	1 ♂	1 ♀			28	6 ♂♂	2 ♀♀	
	C3	3 ♂♂	3 ♀♀			59	1 ♂		
	16	3 ♂♂							
	3	10 ♂♂	13 ♀♀	5 juv.					
	143			2 juv.					
	P16		1 ♀						
	P13	1 ♂							
	P29	1 ♂	1 ♀						
	P30	2 ♂♂	2 ♀♀						
	P34	4 ♂♂	3 ♀♀						
	P37		1 ♀						
	P38	8 ♂♂	11 ♀♀	1 ovig. ♀					
	P42		1 ♀						
	P46	1 ♂							
	P49	1 ♂	5 ♀♀						
	P50		2 ♀♀						

Remarks

P. nitida can be separated from *P. ungulata*, with which it was for many years confused, by the structure of the pleotelsonic apex (distal corners rounded, separated by shallow concave distal margin in *P. nitida*, distal corners acute and spinose, with more concave distal margin in *P. ungulata*), the uropodal ramus (distinctly broader than long in *P. nitida*, as long as wide in *P. ungulata*), and the shape of the coxal plates of the last four pereional segments. (See fig. 2A, C, E.)

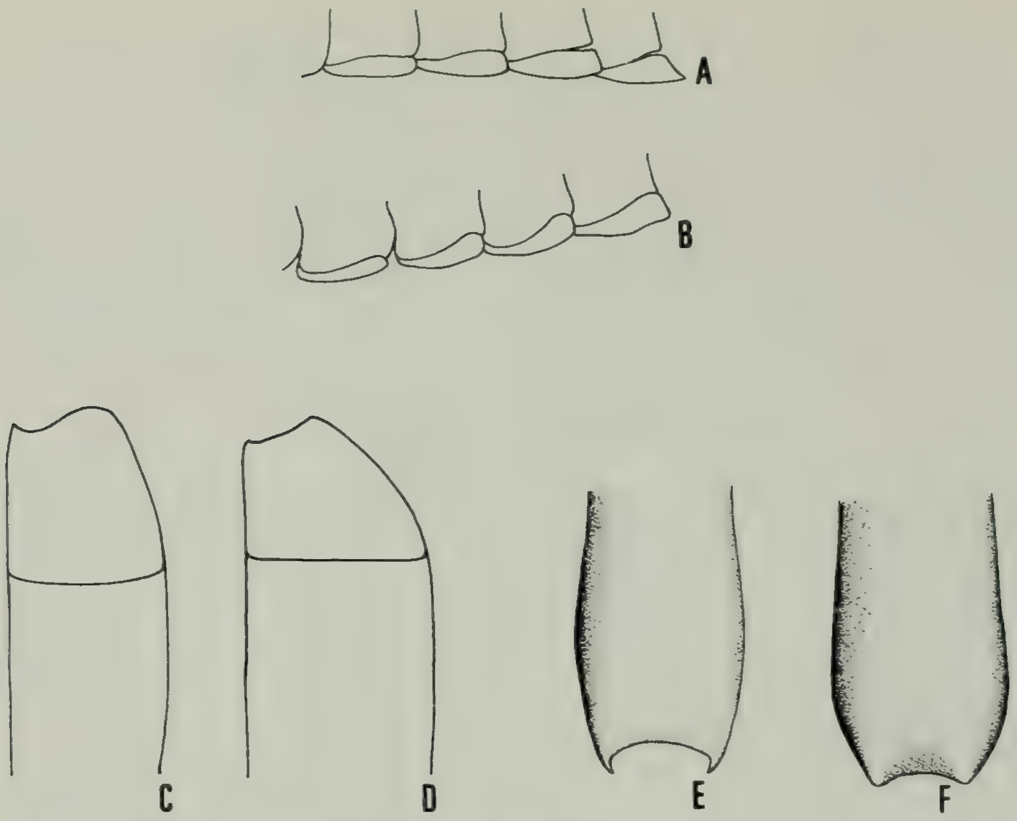

Fig. 2. *Paridotea ungulata* (Pallas).
A—Four posterior coxal plates; C—Uropodal ramus; E—Pleotelsonic apex.
Paridotea nitida (Heller).
B—Four posterior coxal plates; D—Uropodal ramus; F—Pleotelsonic apex.

Separation of *P. nitida* from *P. apposita* Barnard, 1965, recorded from Gough Island, however, is more difficult. The pleotelsonic structure is identical in these two species, the uropodal ramus very similar (possibly not as wide in *P. apposita* as in *P. nitida*), while the seventh pereional coxal plate is perhaps more acute and produced in *P. apposita*. These differences, however, are very subtle, and more material from Gough Island may well prove the species to be synonymous, the subtle differences being a reflection of the isolation of the population.

Paridotea reticulata Barnard

Paridotea reticulata Barnard, 1914: 424, pl. 36D; 1940: 507; 1955: 6.

Previous records

Lüderitzbucht, Port Nolloth, Lamberts Bay, Table Bay, False Bay.

Material

AMS	23	1 ♂				St Paul	32	6 ♀♀	1 ovig. ♀
	79	8 ♂♂	15 ♀♀	3 juv.					
	100	4 ♂♂	5 ♀♀	1 ovig. ♀	7 juv.				

Remarks

The notch found on the sternum of the seventh pereional segment in South African specimens is not present in specimens from the St Paul and Amsterdam Islands. The spines of the disto-lateral corner of the pleotelson are sometimes absent, possibly worn away.

Suborder ANTHURIDEA

Family **Anthuridae**

Eisothistos crateris sp. nov.

Fig. 3A–G

Description

Male: (head and mouthparts damaged). Head with anterior margin between eyes evenly convex, about half length of pereional segment I, with poorly defined median ridge. Pereional segments I–III subequal, each with anterior 'shoulder' and medio-dorsal ridge not quite reaching anterior margin. Pereional segments IV–VII posteriorly expanded, rounded, also with medio-dorsal ridge. Segment VII somewhat shorter than preceding segments. Dorso-lateral keels obvious on anterior three segments only. Anterior three pleonal segments wider than long, laterally rounded, 4th and 5th segments not distinct, possibly fused, much shorter and narrower than preceding segments.

Eyes well developed, ocelli large, distinct.

Antennular peduncle consisting of three stout segments, distal segment bearing pad of elongate setae; flagellum 6-segmented.

Antennal peduncle consisting of two short proximal segments plus two slender elongate segments; flagellum 6-segmented.

Pereiopod I dactylus with well-developed unguis; propodus two and a half times longer than wide, ventral margin bearing single distal spine plus 10 small serrate spines; carpus short, triangular.

Following pereiopods essentially similar to pereiopod I, but with carpi slightly longer, not underriding the propodi.

Pleopod 2 with elongate rami, exopod carrying six slender setae, endopod with four setae and sabre-shaped stylet on inner margin reaching well beyond apex of ramus, apically acute.

Uropods and telson indurated. Uropodal exopod tripartite, consisting of inner rounded basal process armed with three to four small spines, median spike-like elongate portion and outer spine-like process; endopod just reaching apex of telson, apically acute, margins dentate.

Telson evenly rounded, distally wider than proximally, latero-distal margins serrate; strong flattened medio-dorsal keel present, bearing three or four small spines distally.

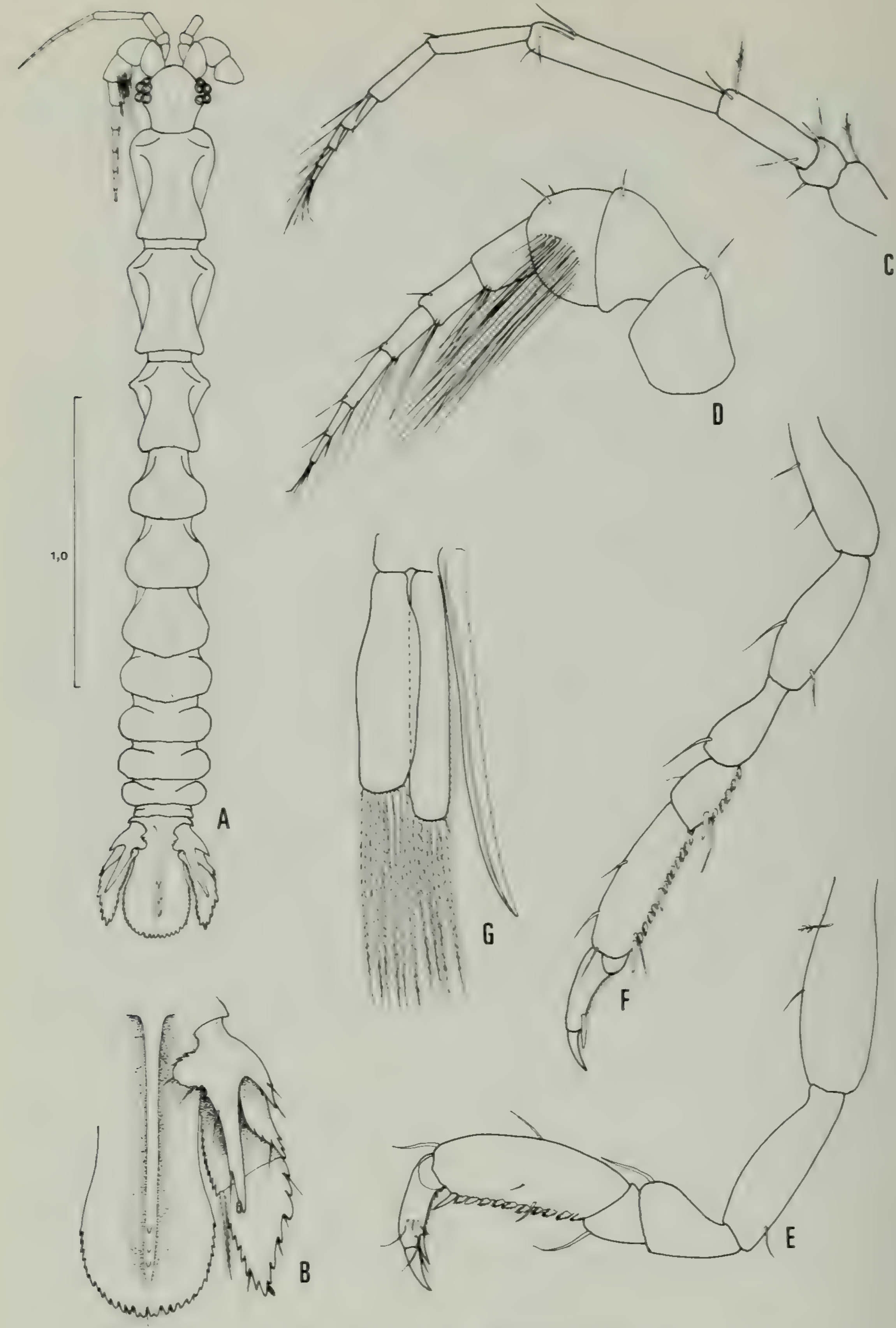

Fig. 3. *Eisothistos crateris* sp. nov.
A—Holotype in dorsal view; B—Telson and uropod; C—Antennule; D—Antenna; E—Pereiopod I; F—Pereiopod VII; G—Pleopod 2.

Material

Holotype: St Paul 90 1 ♂. Paris Museum Is. 1001

Remarks

Of the three species of *Eisothistos* described, *E. vermiformis* Haswell and *E. atlanticus* Vanhöffen are easily separated from the present species, either by general body shape, or on the nature of the telson. There is a marked resemblance to *E. antarcticus* Vanhöffen 1914. The telson of the Antarctic species differs from the present species in having the medio-dorsal ridge armed with numerous spines (instead of four obscure spines), and in the outer process of the uropodal exopod, which is blunt and dentate (rather than spiniform). These differences could perhaps be due to variation within the same species. Another obvious difference is in the pleonal structure. The present specimen has the anterior three pleonal segments large and laterally rounded and the posterior segments obscure, while in *E. antarcticus* the anterior five pleonal segments are subequal.

The species is named *crateris* as it was collected from the crater of St Paul Island which is open to the sea.

Panathura amstelodami sp. nov.

Figs 4A–H, 5A–F

Description

Male: Anterior margin of head with median point; eye spots lateral. Pereional segment I twice length of head, segment II slightly shorter than I, segments III–VI subequal, VIIth somewhat shorter. Pleonal segments distinct. Antennule with 5-segmented peduncle, two basal segments as broad as long, 3rd and 4th segments subequal, wider than long, 5th segment more elongate, flagellum 4-segmented. Antenna with 3-segmented peduncle, 3-segmented flagellum. Mandibular palp 3-segmented, 1st and 3rd segments subequal, each about half length of middle segment; third segment bearing row of 7 spines, proximal 4 spines short; incisor portion of mandible consisting of three strong teeth plus thin plate with dentate margin.

Maxilla slender, bearing 6 spines.

Maxillipedal palp 4 or 5-segmented, 3rd segment largest, endite extending on inner margin to distal level of 3rd palp segment, distally tapered.

Pereiopod I propodus with strong proximal triangular tooth forming a 'thumb', palm with two smaller proximal and one distal tooth; unguis of dactylus large and well-defined.

Pereiopod II more slender and longer than I, palm with strong proximal 'thumb' and small tooth at base, larger distal tooth; carpus with two spines on ventral margin. Pereiopods III–VII similar, propodus twice length of carpus, both segments bearing ventral fringed spines; carpus hardly underriding propodus.

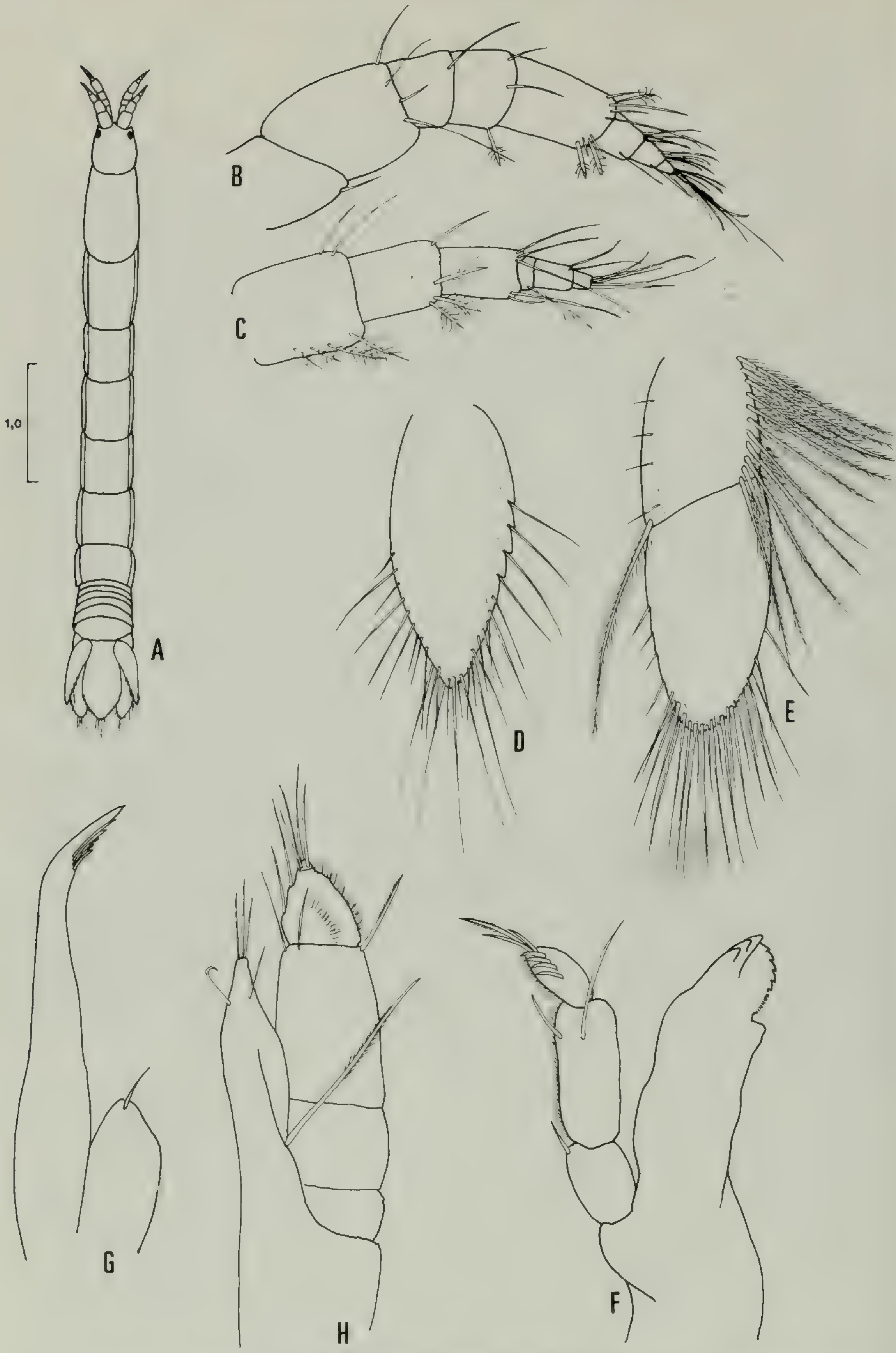

Fig. 4. *Panathura amstelodami* sp. nov.
A—Holotype in dorsal view; B—Antenna; C—Antennule; D—Uropodal exopod; E—Uropodal basis and endopod; F—Mandible; G—Maxilla; H—Maxilliped.

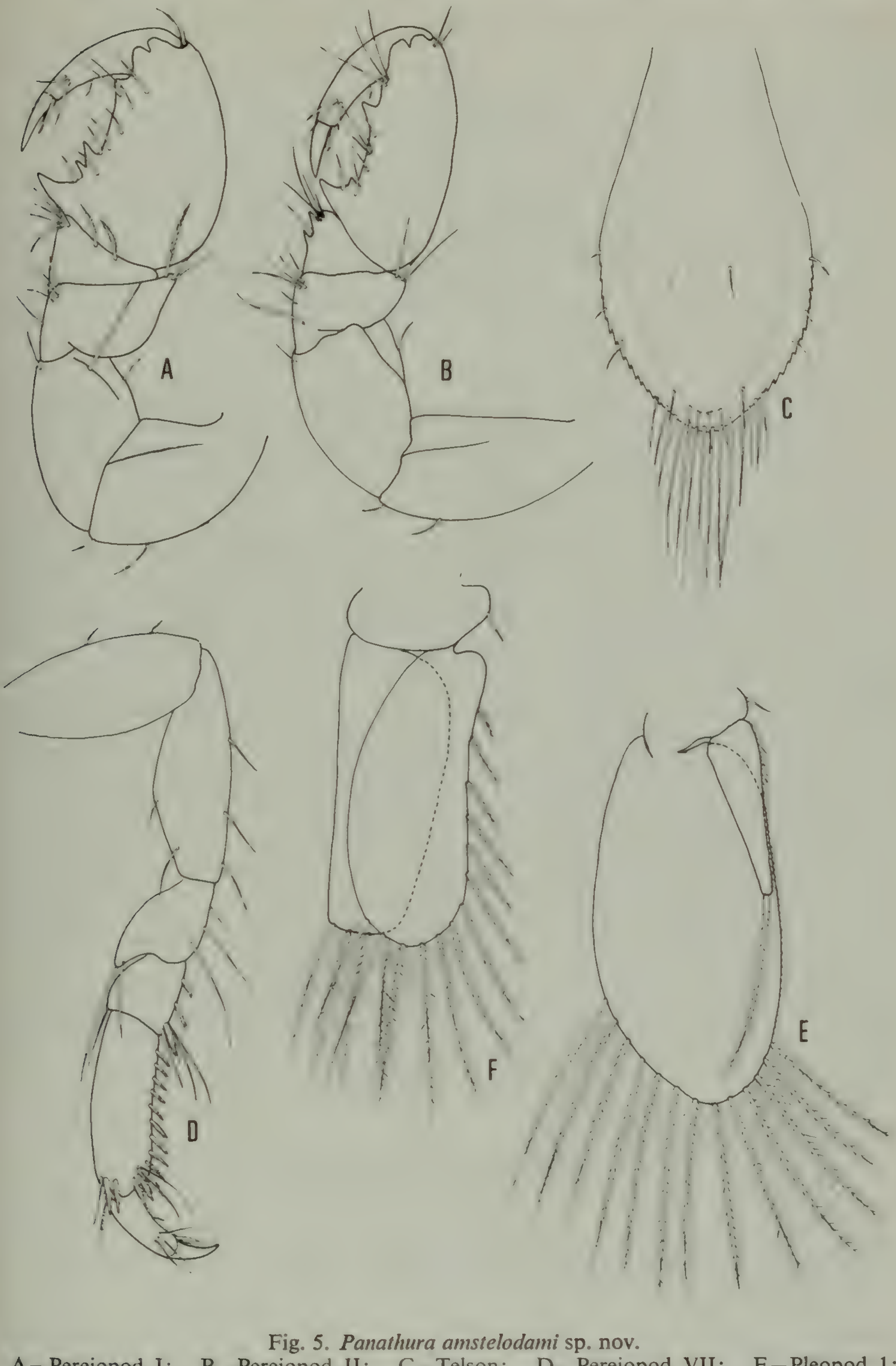

Fig. 5. *Panathura amstelodami* sp. nov.
A—Pereiopod I; B—Pereiopod II; C—Telson; D—Pereiopod VII; E—Pleopod 1; F—Pleopod 2.

Pleopod 1 exopod broad, operculiform, fringed with 13–14 plumose setae; endopod less than half length of exopod, very narrow, triangular, with single terminal plumose seta.

Pleopod 2 exopod and endopod equal in length, former distally truncate, latter distally rounded.

Uropodal exopod leaf-shaped, bearing numerous marginal setae, outer margin with four to five serrations in hyaline border; endopod with distal segment longer than proximal, with hyaline border non-serrate.

Telson widest in distal half, with broad hyaline border, latter finely dentate distally, apical region bearing numerous simple setae.

Material

Holotype	AMS	a4	1 ♂	total length		5,0 mm	Paris Museum Is. 1002
Paratypes	AMS	119	3 ♀♀	3,0 mm	3,2 mm	4,4 mm	SAM–A14994
Paratypes	AMS	142b	2 ♀♀	3,2 mm	3,8 mm		Paris Museum Is. 1003

Remarks

Barnard (1925*b*) defines *Panathura* as similar to *Apanthura*, but possessing a 6-segmented maxilliped and with the palm of pereiopod I straight. The distinctive maxilliped, together with the distinct pleonal segments, operculiform 1st pleopods, and the 5th segment of pereiopods IV–VII underriding the 6th segment, complete the generic definition. The present material agrees with all these features, with the possible exception of the pereiopodal carpi, which only just underride the propodi. The present species differs from *P. serricauda*, with which it was collected, on several counts. The telson and uropods in Barnard's species are indurated and obviously serrated, and the uropodal exopod is a broad structure. In *P. amstelodami* the telson and uropods are not indurated, and possess a thin hyaline border, the exopod is a leaf-shaped structure, and although slightly serrate on the outer margin does not approach the almost dentate condition in *P. serricauda*. Further differences may be seen in the pereiopodal structure, as well as in the 1st pleopod with its reduced endopod. *P. formosa* Menzies & Frankenberg (1966), recorded from deep water off Georgia, U.S.A. possesses a very distinctive pleotelsonic structure, while the endite is not as developed as in the present species.

Panathura serricauda (Barnard)

Fig. 6A–D

Apanthura serricauda Barnard, 1920: 339, pl. 15 (figs 11–12).
Panathura serricauda: Barnard, 1940: 490, 497; 1955: 5.

Previous records

Lüderitzbucht, Saldanha Bay, Table Bay, False Bay.

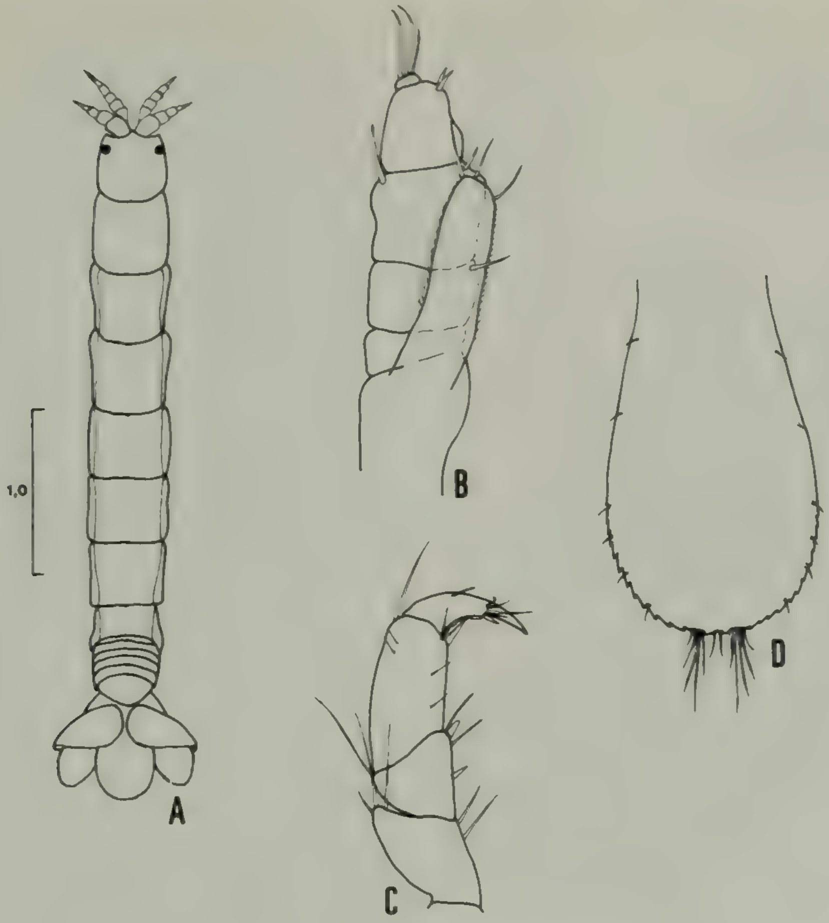

Fig. 6. *Panathura serricauda* (Barnard).
A—Animal in dorsal view; B—Maxilliped; C—four distal segments of pereiopod I; D—Telson.

Material

AMS	a4	7 ovig. ♀♀ + 20 specimens	St Paul	90	2 specimens
	a5	1 specimen			
	a6	1 specimen			

Suborder FLABELLIFERA

Family **Cirolanidae**

Cirolana rugicauda Heller

Cirolana rugicauda Heller, 1861: 497; 1865: 142, pl. 12 (fig. 13). Brocchi, 1877: 99. Hansen, 1890: 358. Vanhöffen, 1914: 503, fig. 40. Barnard, 1940: 397, fig. 8.

Previous records

St Paul Island, Port Nolloth, St Helena Bay.

Material

AMS			
a1			1 juv.
a2			1 juv.
a3			1 juv.
a4	19 ♂♂	33 ♀♀	sev. juv.
a5		6 ♀♀	
a6			sev. juv.
a7		3 ♀♀	5 juv.
a8	4 ♂♂	4 ♀♀	
a9			2 juv.
a10	1 ♂	8 ♀♀	
b3			1 juv.
C1	1 ♂	2 ♀♀	2 juv.
C3		1 ♀	3 juv.
P46		1 ♀	
6b	1 ♂	4 ♀♀	2 juv.
8	1 ♂	1 ovig. ♀	sev. juv.
10		1 ♀	
24a	2 ♂♂	1 ♀	sev. juv.
2.5.1969		1 ♀	
27.3.1970/b	3 ♂♂	6 ♀♀	

St Paul				
6c	2 ♂♂	3 ♀♀		7 juv.
7a	1 ♂	3 ♀♀		5 juv.
7b	9 ♂♂	10 ♀♀		6 juv.
8a	10 ♂♂	20 ♀♀	1 ovig. ♀	sev. juv.
8b	2 ♂♂	4 ♀♀		6 juv.
8c				7 juv.
14	1 ♂			1 juv.
22a				1 juv.
24b	1 ♂	6 ♀♀		sev. juv.
30a	3 ♂♂	8 ♀♀		sev. juv.
30b		4 ♀♀		8 juv.
90	17 ♂♂	10 ♀♀		
93	4 ♂♂	11 ♀♀		4 juv.

Family **Sphaeromatidae**

Cymodocella sapmeri sp. nov.

Figs 7A–G, 8A–E, 9A–E

Description

Body two and one third times longer than wide, widest at VIIth pereional segment; head and pereional segments I–VI smooth; posterior margin of VIIth segment slightly nodose; pleon segment 1 usually concealed by pereion; last pleonal segment bearing irregular row of ten to twelve small conical tubercles. Pleotelson very convex, bearing numerous tubercles, some rounded, most conical. Apex of pleotelson forming dorsally flexed tube, the opening of which has tiny spike or papilla protruding into it. Coxal plates of pereional segments bearing pile of short hairs.

Epistome Λ-shaped, with slender rami.

Antennules shorter than antennae, with 3-segmented peduncle longer than flagellum. Antennal peduncle 5-segmented, distal segment longest; flagellum of about twenty-two segments, longer than peduncle.

Mandibular palp 3-segmented, terminal segment with thirteen pectinate setae, middle segment with eight pectinate setae; incisor process of four teeth, lacinia mobilis of three teeth; setal row of eight penicilis; molar process broad, with dentate margin.

Inner ramus of first maxilla bearing four elongate fringe setae, plus shorter simple seta; outer ramus tipped with eight dentate spines, degree of dentition varying from fairly smooth to many large denticles.

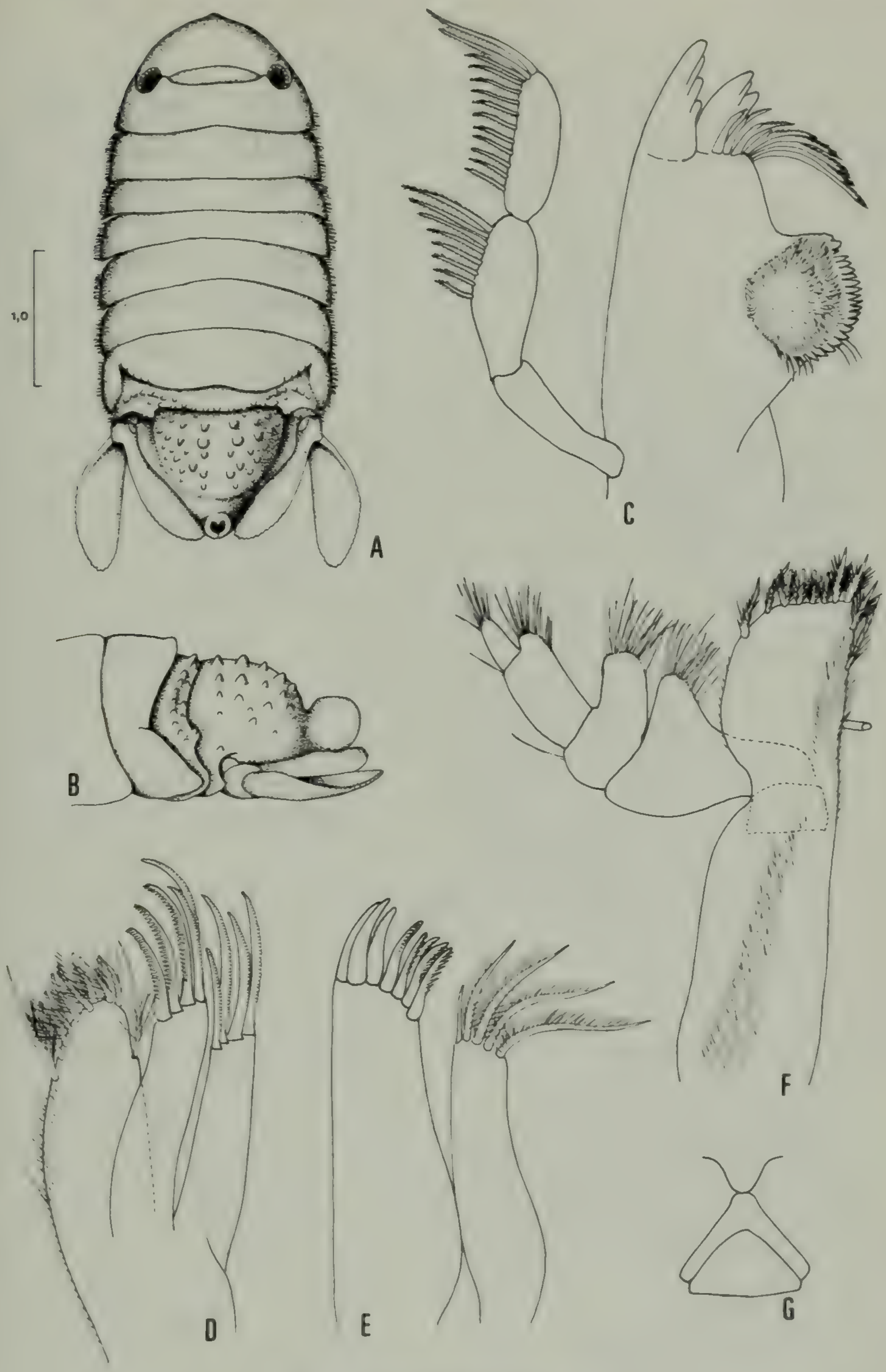

Fig. 7. *Cymodocella sapmeri* sp. nov.
A—Holotype in dorsal view; B—Pleotelson in lateral view; C—Left mandible; D—Second maxilla; E—First maxilla; F—Maxilliped; G—Epistome.

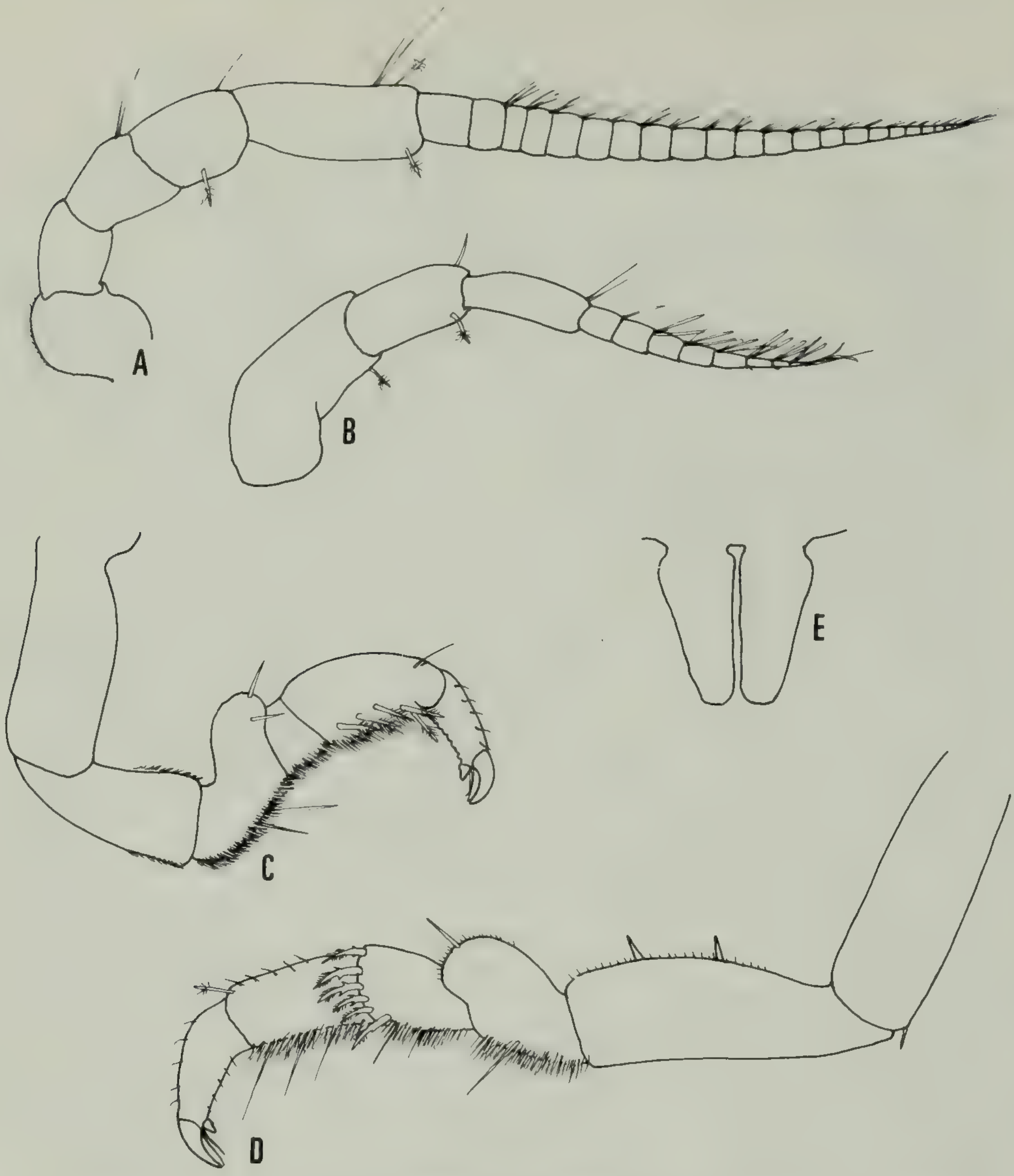

Fig. 8. *Cymodocella sapmeri* sp. nov.
A—Antenna; B—Antennule; C—Pereiopod I; D—Pereiopod VII; E—Penes.

Second maxilla, inner ramus with about ten fringed spines, both lobes of outer ramus tipped with four or five pectinate curved spines.

Maxillipedal palp 5-segmented, second segment longest; segments two, three and four somewhat lobed, lobes bearing clumps of simple setae; endite bearing about ten fringed spines, and single coupling hook.

Pereiopod I with propodus, carpus, merus, and distal part of ischium bearing pile of fine short setules; propodus bearing five fringed spines; carpus very short; dactylus tipped with distal curved spine with shorter blunt spine at its base. Pereiopods increasing slightly in length posteriorly.

Pereiopod VII with carpus bearing six fringed spines; ischium with two strong spines on dorsal margin.

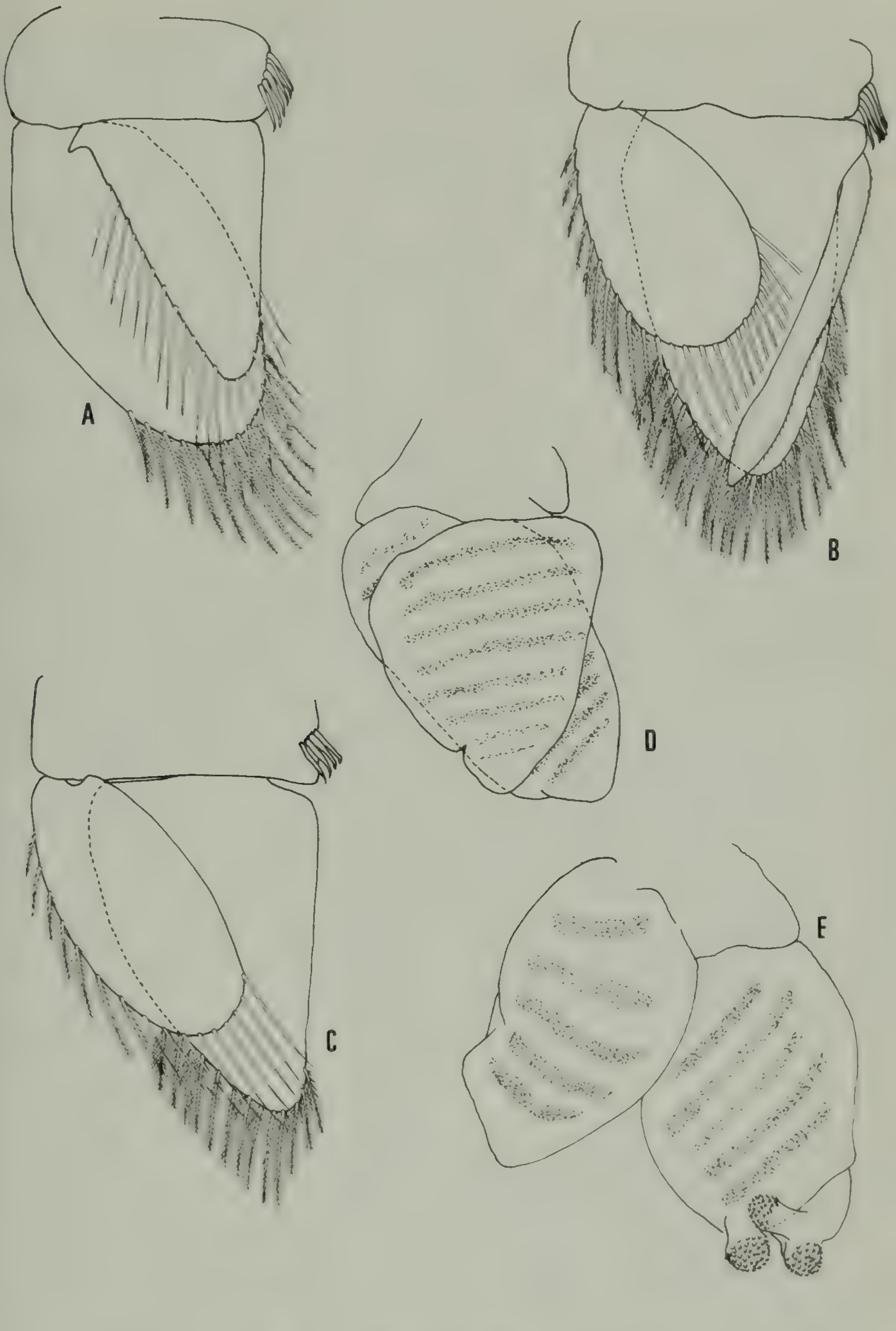

Fig. 9. *Cymodocella sapmeri* sp. nov.
A—Pleopod 1; B—Pleopod 2; C—Pleopod 3; D—Pleopod 4; E—Pleopod 5.

Rami of penis moderately elongate, tapering slightly.

Pleopod 1 exopod broadly oval, longer than triangular endopod.

Pleopod 2 exopod oval, much smaller and shorter than triangular endopod; latter with stylet on median margin, stylet slightly longer than endopod, distally dilated, apically narrowly rounded.

Pleopod 3 with oval exopod shorter than triangular endopod.

Pleopods 4 and 5 with both rami membranous, pleated.

Both rami of uropod elongate-oval, of equal length, distally rounded, margins slightly serrulate.

Pleotelson of female less obviously tuberculate than that of male.

Material

Holotype	AMS	C3	1 ♂			Paris Museum Is. 1004
Allotype	AMS	C2			1 ovig. ♀	Paris Museum Is. 1005
Paratypes	St Paul	D5/c	13 ♂♂	9 ♀♀	6 ovig. ♀♀	Paris Museum Is. 1006
Paratypes	AMS	C1	5 ♂♂	12 ♀♀	14 ovig. ♀♀	SAM–A14995

AMS				
a2		5 ♀♀		1 juv.
a3		1 ♀		1 juv.
a4		3 ♀♀		
a5	1 ♂	1 ♀		
a6		3 ♀♀	1 ovig. ♀	2 juv.
b1		1 ♀		
b2/2		6 ♀♀		6 juv.
C2	5 ♂♂	7 ♀♀	10 ovig. ♀♀	17 juv.
C3	4 ♂♂	1 ♀	3 ovig. ♀♀	7 juv.
P29			1 ovig. ♀	
P30		3 ♀♀		
P33			1 ovig. ♀	
P34			1 ovig. ♀	
P36		2 ♀♀		
3	1 ♂			
6b	2 ♂♂			2 juv.
24a	2 ♂♂	2 ♀♀	1 ovig. ♀	
147				2 juv.
28.3.1970/b	1 ♂	1 ♀		

St Paul				
D/5a		3 ♀♀	1 ovig. ♀	2 juv.
D5/b			1 ovig. ♀	
14	4 ♂♂	10 ♀♀		5 juv.
16	1 ♂	1 ♀		
19			2 ovig. ♀♀	
20	1 ♂	1 ♀	1 ovig. ♀♀	
22b	1 ♂			
28		7 ♀♀	1 ovig. ♀	11 juv.
90	6 ♂♂	16 ♀♀	3 ovig. ♀♀	

Remarks

Of the eleven species of *Cymodocella* described, the present species only resembles *C. nipponica* Nishimura, from Japan, to a limited degree. That Japanese species possesses numerous rounded tubercles on the pleotelson, while the present species possesses more numerous conical tubercles. Apart from this tenuous similarity, *C. sapmeri* is quite distinct from all other described species. This species is named for S.A.P.M.E.R., the lobster-fishing company operating around the St Paul and Amsterdam Islands (see introduction), and for the ship used by the Company.

Dynamenella brunnea Vanhöffen

Fig. 10A–B

Dynamenella brunnea Vanhöffen, 1914: 516, fig. 49. *non Dynamenella huttoni:* Barnard, 1940: 419.

Previous records

St Paul Island.

Material

AMS	a1		1 ♀	
	a3		2 ♀♀	
	a4	2 ♂♂	3 ♀♀	
	a5			2 juv.
	a6		11 ♀♀	sev. juv.
	a7	5 ♂♂		
	a8	2 ♂♂		
	a10	5 ♂♂	2 ♀♀	
	b1		1 ♀	
	b2/2		2 ♀♀	
	c1	1 ♂	14 ♀♀	sev. juv.
	c2		7 ♀♀	
	c3		2 ♀♀	
	P1		1 ♀	
	P2			sev. juv.
	P4			1 juv.
	P6			3 juv.
	P7			2 juv.
	P13b		1 ♀	
	P16	1 ♂		sev. juv.
	P23			2 juv.
	P26			sev. juv.
	P27			4 juv.
	P28			1 juv.
	P29			sev. juv.
	P31			1 juv.
	P30	3 ♂♂	2 ♀♀	sev. juv.
	P36			sev. juv.
	P34			sev. juv.
	P38	1 ♂	4 ♀♀	sev. juv.
	P44			1 juv.
	P45			1 juv.
	P48			2 juv.
	P49			sev. juv.
	P50	3 ♂♂	6 ♀♀	sev. juv.
	P83			7 juv.
	3	3 ♂♂	6 ♀♀	sev. juv.
	8	58 ♂♂	28 ♀♀	
	12	9 ♂♂	1 ♀	
	16		1 ♀	10 juv.
	24a		1 ♀	
	2.5.1969	1 ♂	6 ♀♀	
	1.3.1970	1 ♂	3 ♀♀	
	27.3.1970/b	3 ♂♂		
	28.3.1970/b	4 ♂♂	9 ♀♀	

St Paul	D5/a	2 ♂♂	2 ♀♀	1 juv.
	D5/c		11 ♀♀	sev. juv.
	7b	1 ♂		
	8a			2 juv.
	14	1 ♂		sev. juv.
	20		1 ♀	5 juv.
	26		1 ♀	
	28		3 ♀♀	

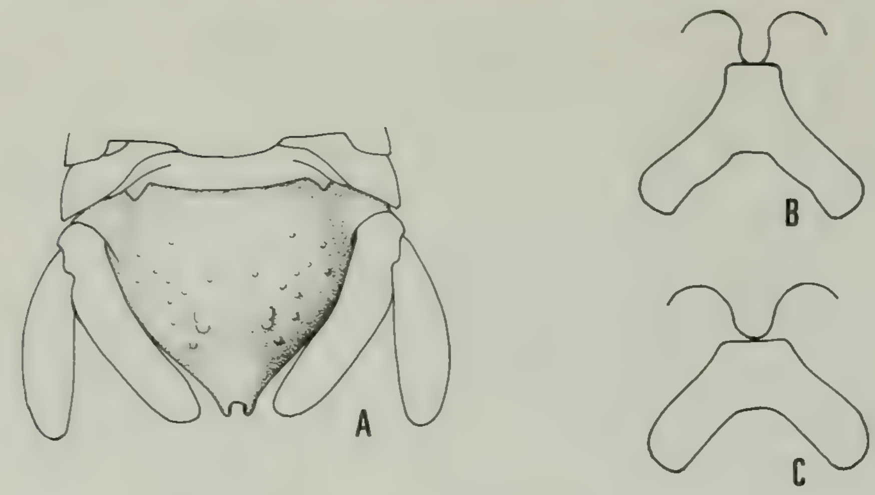

Fig. 10. *Dynamenella brunnea* Vanhöffen.
A—Pleotelson; B—Epistome; C—Epistome of *D. huttoni.*

Remarks

Examination of Vanhöffen's type material in both the Berlin Museum and the British Museum, together with the very large number of specimens in the present collection, shows that this is indeed a valid species. Separation from *D. huttoni* which resembles (and with which Barnard synonymized it) is best done by reference to three features: pleotelsonic structure, epistome and head structure, and colour pattern. The dorsal surface of the pleotelson in *D. brunnea* always has some indication of tuberculation. In juveniles of less than 2 mm length, the two main submedian tubercles can already be seen, while in larger specimens these two large tubercles are supplemented by several smaller tubercles. *D. huttoni* by contrast invariably possesses a smooth pleotelson. The median ventrally-directed lobe of the sinuous frontal margin of the head in *D. brunnea* is relatively narrower than in *D. huttoni*; a subtle difference in the shape of the epistomes is also constant. The colour pattern, though variable in both species, is more constant in *D. brunnea,* where a rhomboidal pale patch is frequently seen mid-dorsally on pereional segments II to IV. While *D. huttoni* often has pale dorsal patches, these almost never are as regular as in the former species.

Dynamenella dioxus Barnard

Dynamenella dioxus Barnard, 1914: 419; 1940: 418, 505. Day, Field & Penrith, 1970: 48.

Previous records

Lüderitzbucht, Port Nolloth, Lamberts Bay, Table Bay, False Bay.

Material

AMS	a4	2 ♂♂	1 ♀		St Paul	D/5a	1 ♂
	74	3 ♂♂	4 ♀♀				
	142a	1 ♂	1 ♀				
	142b	7 ♂♂	18 ♀♀	5 juv.			
	147	1 ♂	1 ♀				

Parisocladus perforatus (H. M. Edwards)

Sphaeroma perforata Edwards, 1840: 211. Heller, 1861: 496; 1865: 139, pl. 12 (fig. 9).
Spheroma perforata: Brocchi, 1877: 97.
Dynamenella perforata: Hansen, 1905: 117, 126.
Cycloidura perforata: Stebbing, 1910: 431. Vanhöffen, 1914: 511, figs 45–46.
Parisocladus perforatus: Barnard, 1914: 402, pl. 32H; 1940: 418, 505. Penrith & Kensley, 1970*a*: 228; 1970*b*: 259. Day, Field & Penrith, 1970: 48.

Previous records

Rocky Point (S.W.A.), Möwe Bay (S.W.A.), Swakopmund, Lüderitzbucht, Port Nolloth, Lamberts Bay, Dyers Island, Table Bay, False Bay, Port Alfred, East London, St Paul Island, Amsterdam Island.

Material

AMS	a1			sev. juv.
	a3	6 ♂♂	8 ♀♀	sev. juv.
	a4	4 ♂♂	6 ♀♀	sev. juv.
	a5		3 ♀♀	
	a7		2 ♀♀	
	a9	1 ♂	1 ♀	
	b2/1a		1 ♀	
	b2/1b		4 ♀♀	sev. juv.
	b2/2	3 ♂♂	3 ♀♀	sev. juv.
	b3	1 ♂		2 juv.
	C2	3 ♂♂	1 ♀	
	C3			2 juv.
	J11			1 juv.
	P2	1 ♂		
	P11	4 ♂♂	7 ♀♀	
	P13a	3 ♂♂	3 ♀♀	
	P13b	2 ♂♂	4 ♀♀	sev. juv.
	P17			6 juv.
	P26			6 juv.
	P28			1 juv.
	P29			6 juv.
	P30			6 juv.
	P33			sev. juv.
	P34			sev. juv.
	P36			sev. juv.
	P39			1 juv.
	P44			7 juv.
	P45			1 juv.
	P46	2 ♂♂		3 juv.
	P47			3 juv.
	P50	1 ♂		
	3	2 ♂♂		sev. juv.
	5a	2 ♂♂	4 ♀♀	sev. juv.
	6b	2 ♂♂	3 ♀♀	
	8	16 ♂♂	5 ♀♀	2 juv.
	9		2 ♀♀	
	12	3 ♂♂		
	14	13 ♂♂	37 ♀♀	sev. juv.
	24a	17 ♂♂	6 ♀♀	sev. juv.
	2.5.1969	1 ♂		
	27.3.1970/b	24 ♂♂	21 ♀♀	3 juv.
	28.3.1970/b	2 ♂♂	5 ♀♀	4 juv.
St Paul	D5/a	1 ♂	36 ♀♀	
	D5/b			1 juv.
	D5/c	5 ♂♂	8 ♀♀	1 juv.
	6a			1 juv.
	6c	12 ♂♂		sev. juv.
	7a	13 ♂♂	3 ♀♀	sev. juv.
	8a	2 ♂♂		4 juv.
	8b	1 ♂		
	14	6 ♂♂		sev. juv.
	15	2 ♂♂		sev. juv.
	16	7 ♂♂		sev. juv.
	18	1 ♂	3 ♀♀	3 juv.
	19	3 ♂♂		sev. juv.
	20			sev. juv.
	22a		1 ♀	2 juv.
	22b			2 juv.
	22c		1 ♀	1 juv.
	23a			sev. juv.
	26	1 ♂	4 ♀♀	
	23	13 ♂♂	10 ♀♀	
	27	1 ♂		4 juv.
	28	3 ♂♂		sev. juv.
	30b	3 ♂♂	1 ♀	
	30g	13 ♂♂	9 ♀♀	
	35		3 ♀♀	
	76	8 ♀♀		9 juv.
	77a		2 ♀♀	
	90		6 ♀♀	
	91	3 ♂♂		sev. juv.

Family **Limnoriidae**

Limnoria (*Limnoria*) *quadripunctata* Holthuis

Limnoria quadripunctata Holthuis, 1949: 167. Menzies & Mohr, 1952: 81. Menzies, 1957: 127. Schultz, 1969: 143.

Previous records

North Sea coast of Holland, California coast, Valparaiso (Chile).

Material

AMS				
a4	1 ♂			
5a		1 ♀	1 ovig. ♀	13 juv.
5b		1 ♀		4 juv.
16.1.1971	2 ♂♂		2 ovig. ♀♀	6 juv.

St Paul			
B19	1 ♂		
77a	6 ♂♂	9 ♀♀	9 ovig. ♀♀
1970	3 ♂♂		4 ovig. ♀♀

Remarks

These specimens were all found in the holdfasts of the giant brown algae *Macrocystis pyrifera* and *Laminaria pallida* from the upper infralittoral zone, with the exception of station B19 on St Paul Island, where the isopods were found in clusters of red algae from a depth of 30 metres.

Family **Cymothoidae**

Lironeca raynaudii (H. M. Edwards)

Livoneca raynaudii: Barnard, 1920: 358; 1940: 501; 1955: 6.

Previous records

Table Bay, Durban, New Zealand, Tasmania, New South Wales, Japan.

Material

St Paul	82	1 ♂
	3.1.1971	1 ♀

Family **Aegidae**

Aega '*antillensis*' Schiödte & Meinert

Aega antillensis: Richardson, 1905: 170. Barnard, 1925*a*: 389. Schultz, 1969: 190.

Previous records

Natal, West Indies, Japan.

Material

St Paul	3.1.1971	1	from fishing-boat
	3.1.1971	1	on *Thyrsites atun*

Remarks

Slight differences in the frontal laminae, telson, etc., suggest that *A. antillensis s.s.*, and specimens from South Africa, and others from St Paul Island are not all the same species, although all keyed out to this species.

Aega monilis Barnard

Aega monilis Barnard, 1914: 365, pl. 31C; 1940: 500.

Previous records

Table Bay, off Cape Peninsula, off East London.

Material

St Paul	85	1 ovig. ♀

Remarks

It seems probable from the brief description provided by Brocchi (1877: 100) of *Rocinela major*, from St Paul Island, that this was a specimen of *Aega monilis*. Examination of Brocchi's type, however, is necessary to establish the identity of *R. major*

Suborder ASELLOTA

Family **Stenetriidae**

Stenetrium crassimanus Barnard

Stenetrium crassimanus Barnard, 1914: 217; 1940: 510. Wolff, 1962: 23.

Previous records

False Bay (Cape), Natal.

Material

St Paul	18	1 ♂
	91	2 ♂♂

Stenetrium saldanha Barnard

Fig. 11A–F

Stenetrium saldanha Barnard, 1920: 403. Wolff, 1962: 24, 29.

Previous records

Saldanha Bay, False Bay, Still Bay.

Material

AMS	D1	1 ♂	1 ♀	St Paul	18		1 ♀	1 ovig. ♀
	142b	1 ♂	1 ♀		91	1 ♂	1 ♀	

Remarks

Wolff's key (1962: 22), taken from Barnard's description of *S. saldanha*, places this species in the group which lacks any process at the antero-lateral corner of the first antennal peduncle segment. This segment, however is produced into a triangular process which is sometimes difficult to see.

Family **Antiasidae**

Antias dimorphus Menzies

Antias dimorphus Menzies, 1962: 63, fig. 16.

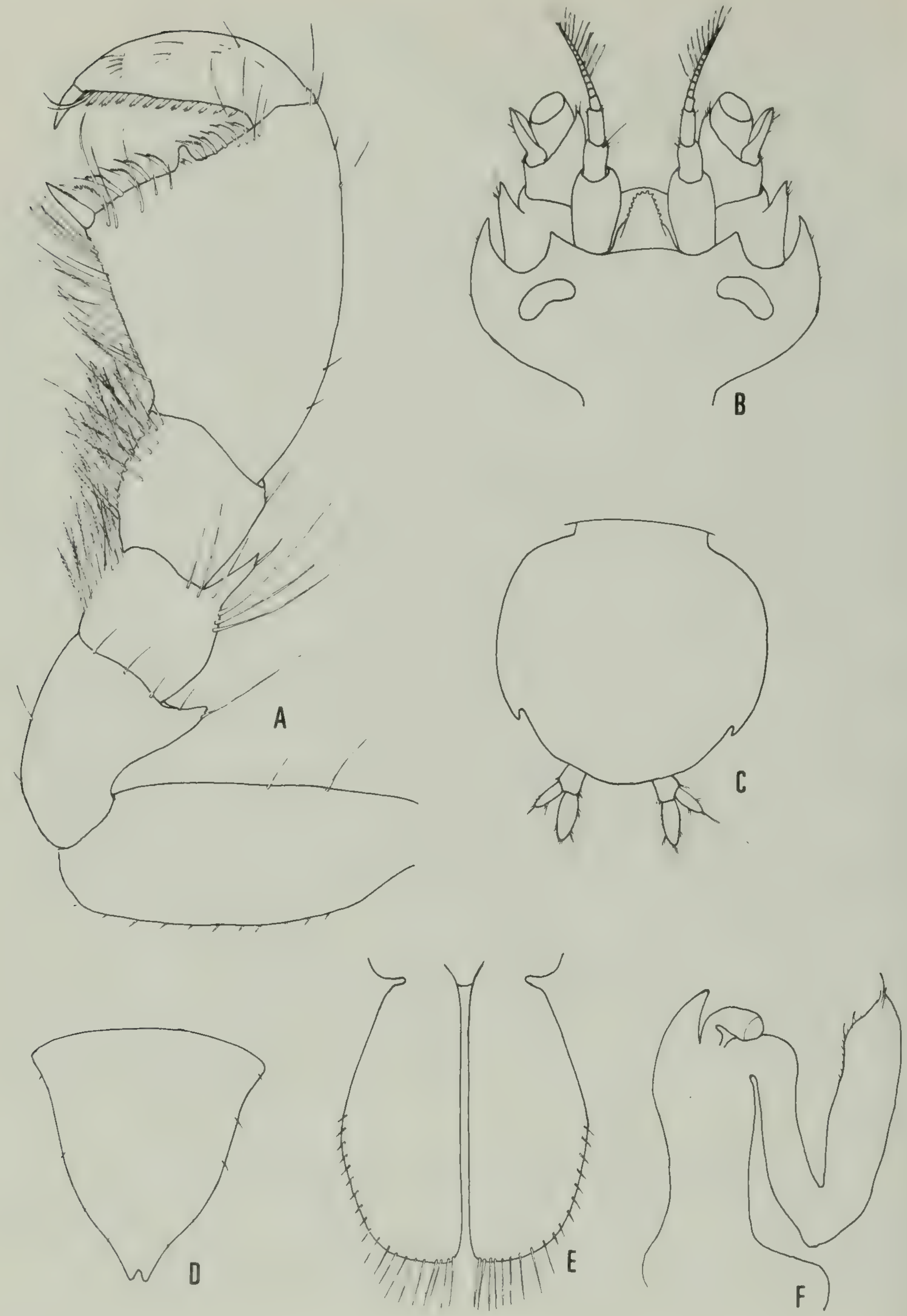

Fig. 11. *Stenetrium saldanha* Barnard .
A—Pereiopod I; B—♀ head in dorsal view; C—Pleotelson; D—Operculum ♀; E—Pleopod 1 ♂; F—Pleopod 2 ♂.

Previous records

Southern Chile, Kerguelen Island.

Material

AMS	a1	15 ♂♂	16 ♀♀	14 ovig. ♀♀	St Paul	D3	1 ♂		
	a2	5 ♂♂		2 ovig. ♀♀		8a	42 ♂♂	9 ♀♀	24 ovig. ♀♀
	a3	5 ♂♂	4 ♀♀	3 ovig. ♀♀		8b	3 ♂♂		1 ovig. ♀
	C2	9 ♂♂	2 ♀♀	5 ovig. ♀♀		8c	16 ♂♂	16 ♀♀	5 ovig. ♀♀
	C3	2 ♂♂	1 ♀	3 ovig. ♀♀		14	1 ♂		2 ovig. ♀♀
	6b	1 ♂				90			2 ovig. ♀♀
						93	26 ♂♂	9 ♀♀	10 ovig. ♀♀

Remarks

Amongst Vanhöffen's material of *Antias marmoratus* collected by the Südpolar Expedition at Kerguelen Island (Berlin Museum 17699) are four specimens of *Antias dimorphus* showing the enlarged first pereional segment. The remaining specimens of *A.* '*marmoratus*' from Kerguelen at St Paul Island collected by the Südpolar Expedition are probably *A. hofsteni* Nordenstam. As Vanhöffen's material is a mixture of two species, each from a different location, the name *A. marmoratus* will be omitted from the faunal list of the two islands, but remains on the list of species for Kerguelen Island.

Antias hispidus Vanhöffen
Fig. 12A–B

Antias hispidus Vanhöffen, 1914: 533, fig. 60. Stephensen, 1927: 356, fig. 24. Nordenstam, 1933: 201, fig. 47. Menzies & Miller, 1955: 385.

Previous records

St Paul Island, Auckland Island, Falkland Island, Graham region (Antarctica).

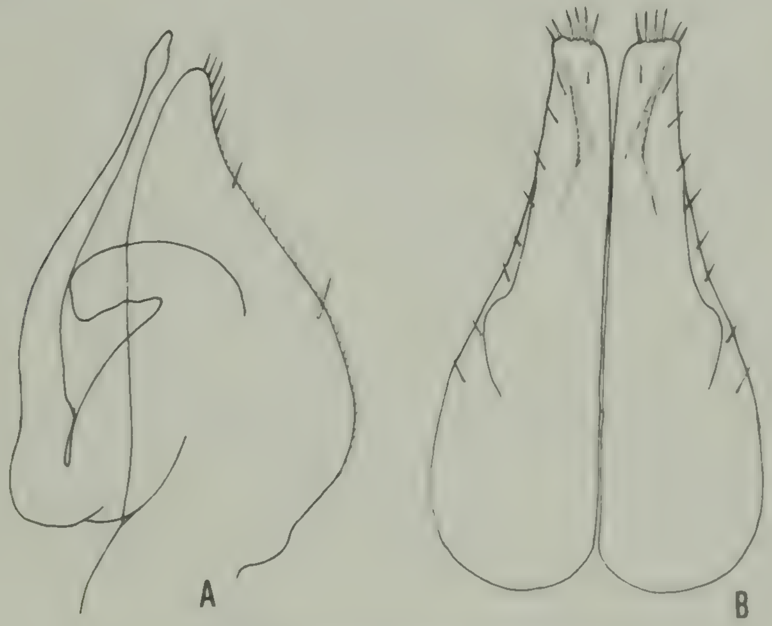

Fig. 12. *Antias hispidus* Vanhöffen.
A—Pleopod 2 ♂; B—Pleopod 1 ♂.

Material

AMS	a6	1 ♂	1 ♀		St Paul	8a	7 ♂♂	7 ♀♀	6 ovig. ♀♀
	a4	6 ♂♂	1 ♀	3 ovig. ♀♀		8b			1 ovig. ♀
	b3	2 ♂♂	1 ♀			14	1 ♂		
	D12		1 ♀			16		2 ♀♀	1 ovig. ♀
	173	1 ♂				77a	1 ♂		
						93	3 ♂♂	2 ♀♀	4 ovig. ♀♀

Antias hofsteni Nordenstam

Fig. 13

Antias hofsteni Nordenstam, 1933: 205. Menzies & Miller, 1955: 385. Menzies, 1962: 60.

Previous records

South Georgia.

Material

AMS	17.1.1971	1 ♂	1 ovig. ♀	St Paul	29.1.1971	1 ♀	
	D19	1 ♂			B7		1 ovig. ♀
	119	1 ♂	1 ovig. ♀				
	142b		1 ovig. ♀				

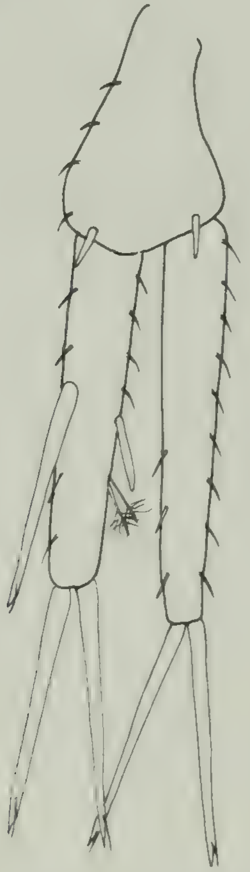

Fig. 13. *Antias hofsteni* Nordenstam.
Uropod.

Remarks

In the general body structure and proportions, and in the appendages, the present material agrees completely with Nordenstam's description. The uropod, which was lacking in all the Antarctic material previously collected, is figured.

Family **Janiridae**

Caecianiropsis ectiformis (Vanhöffen)

Fig. 14A–C

Austroniscus ectiformis Vanhöffen, 1914: 553, fig. 80.
Caecianiropsis ectiformis: Menzies & Pettit, 1956: 446.

Previous records

Observatory Bay, Kerguelen Island.

Material

St Paul 90 1 ♀ Total length 1,5 mm

Remarks

Vanhöffen's figure does not show the first pleonal segment. This segment, although difficult to see, is present in both the Kerguelen and St Paul specimens.

Ianiroides gen. nov.

Diagnosis

Janirid possessing eyes, slight rostral point, scale on antennal peduncle. Pereional segments more or less equal in length and width. Coxal plates dorsally visible on all segments. Pleon longer than wide.

Pereiopod I similar in male and female; propodus distally expanded, palm straight; dactylus biunguiculate.

Pereiopods II–VII triunguiculate.

Uropod with well-developed basis, exopod half length and width of endopod.

Pleopod 1 in male narrow, Y-shaped, proximal halves of rami contiguous, distal halves divergent, narrow.

Discussion

In the structure of the antennae and mouthparts, the rostral projection, the prehensile first pereiopod, the triunguiculate dactyli of the remaining pereiopods, this species could be placed into the genus *Janira*, as Barnard (1920) did. The Y-shaped first pleopod of the male, however, which resembles no other janirid, demands the creation of a new genus. The type species of the genus is *Ianiroides angusta* (Barnard, 1920), and was originally described from a single male from False Bay, Cape. Some of the appendages of this specimen have been refigured.

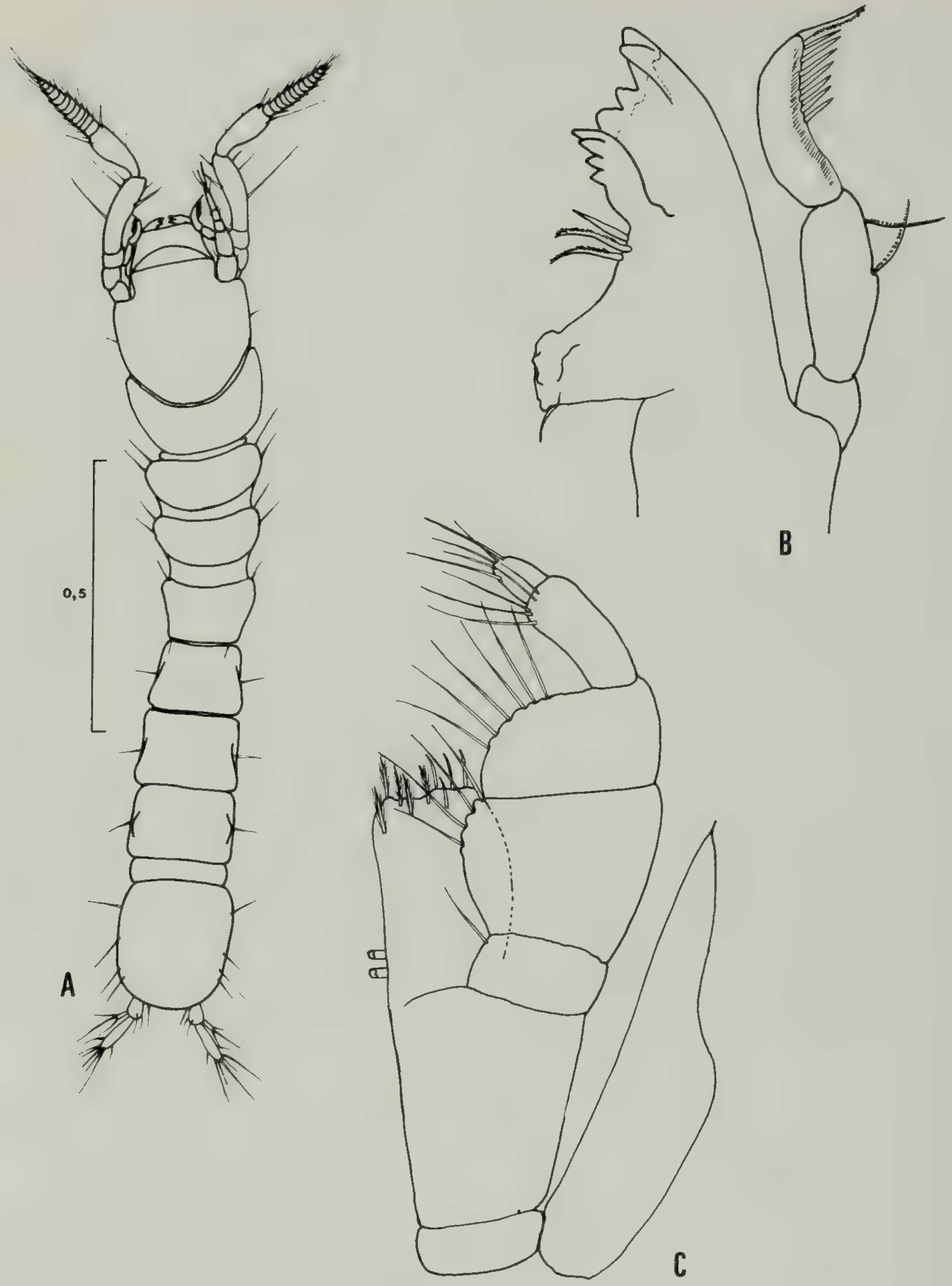

Fig. 14. *Caecianiropsis ectiformis* (Vanhöffen).
A—♀ in dorsal view; B—Mandible; C—Maxilliped.

Ianiroides angusta (Barnard)

Figs 15A–F, 16A–D

Janira angusta Barnard, 1920: 404, pl. 17 (figs 1–3); 1940: 511. Wolff, 1962: 41.

Previous records

False Bay, Cape 1 ♂.

Material

AMS	74	3 ♀♀	1,5 mm	1,8 mm	2,0 mm

Supplementary description

Eyes with nine or ten ocelli. Coxal plates visible on all pereional segments, those on segments I–IV situated at antero-lateral corners, those on segments V–VII on postero-lateral corners; coxal plates of segments I and II distally acute, remaining plates rounded.

Pereiopod I similar in male and female, with propodus distally broad, palm armed with five or six short blunt sensory setae; dactylus apically biunguiculate.

Operculum in female broader than long, with distal margin slightly concave.

Pleopod 1 in male narrow, rami proximally contiguous, distally divergent, apically tapered, tipped with several setae.

Ianisera gen. nov.

Diagnosis

Janirid possessing eyes, no distinct rostral point; scale on antennal peduncle; antennule well developed. Pereional segments more or less equal in length and width. Coxal plates dorsally visible on all segments. Maxillipedal palp 5-segmented, three proximal segments expanded. Pereiopods similar, ambulatory, dactyli all biunguiculate. Uropodal basis short, rami separate, exopod slightly shorter and narrower than endopod. First pleopod of male very broad, expanded, rami fused proximally. Pleotelson marginally serrate, bearing dorso-lateral ridge. The type species of the genus is *Ianisera trepidus* sp. nov.

Remarks

The presence of eyes, well-developed antennules, uropods, and molar process of the mandible, together with the enlarged segments of the maxillipedal palp, all the pereiopods being ambulatory, and the body parallel-sided, suggest the group of genera *Jaera*, *Janira*, *Janilirata*, *Ianiropsis*. The first pereiopods of the male are not more elongate than the following pereiopods as in *Ianiropsis*, or prehensile as in *Janira*, neither are the uropods produced well beyond the body margin as in *Janilirata*, nor does the species possess indented lateral margins of the posterior pereional segments. This species is characterized by the broad first pleopod of the male, the pleotelson bearing a lateral ridge, and all the pereiopods armed with two dactylar spines.

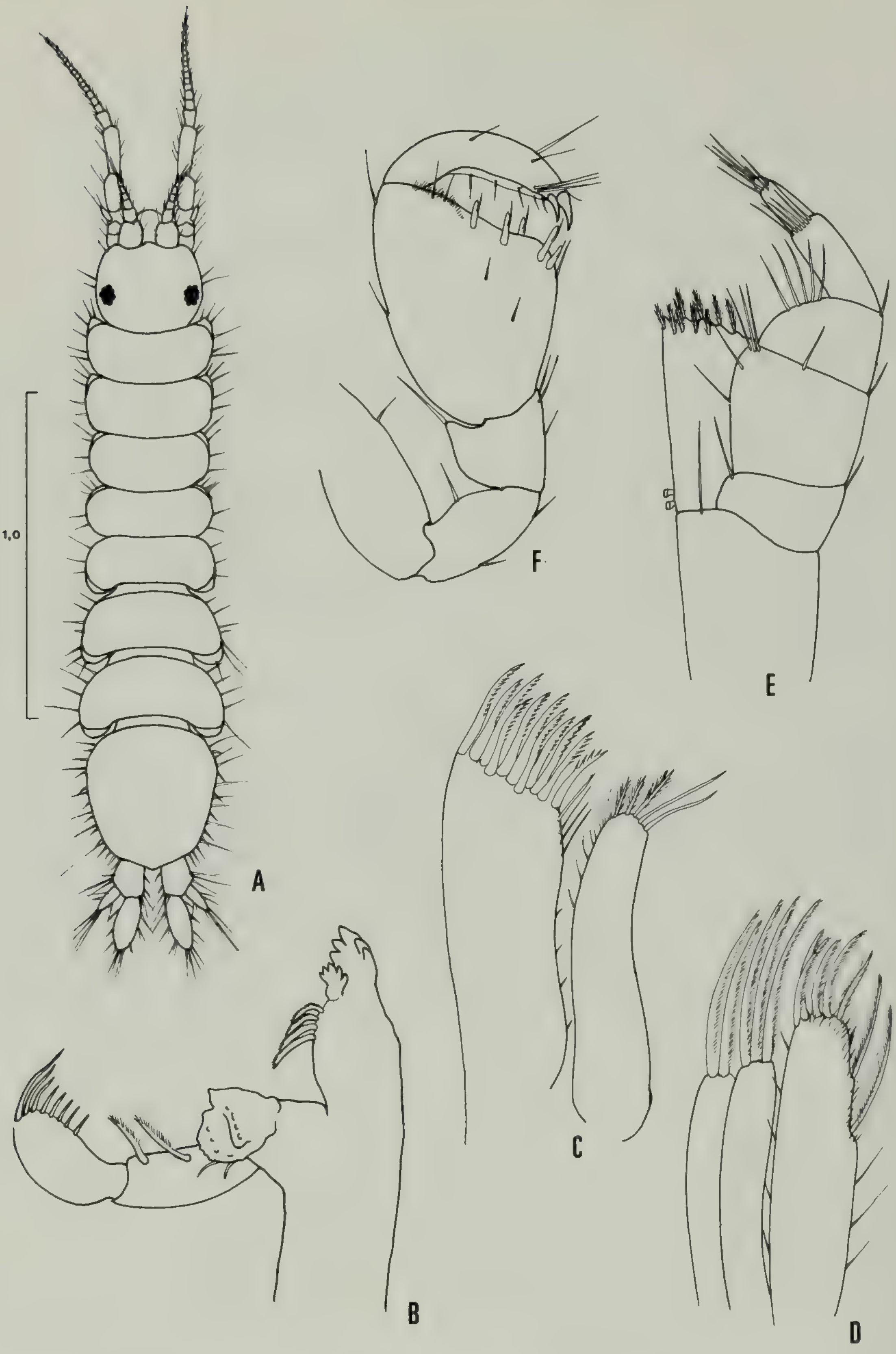

Fig. 15. *Ianiroides angusta* (Barnard).
A—♀ in dorsal view; B—Mandible; C—First maxilla; D—Second maxilla; E—Maxilliped; F—First pereiopod ♀.

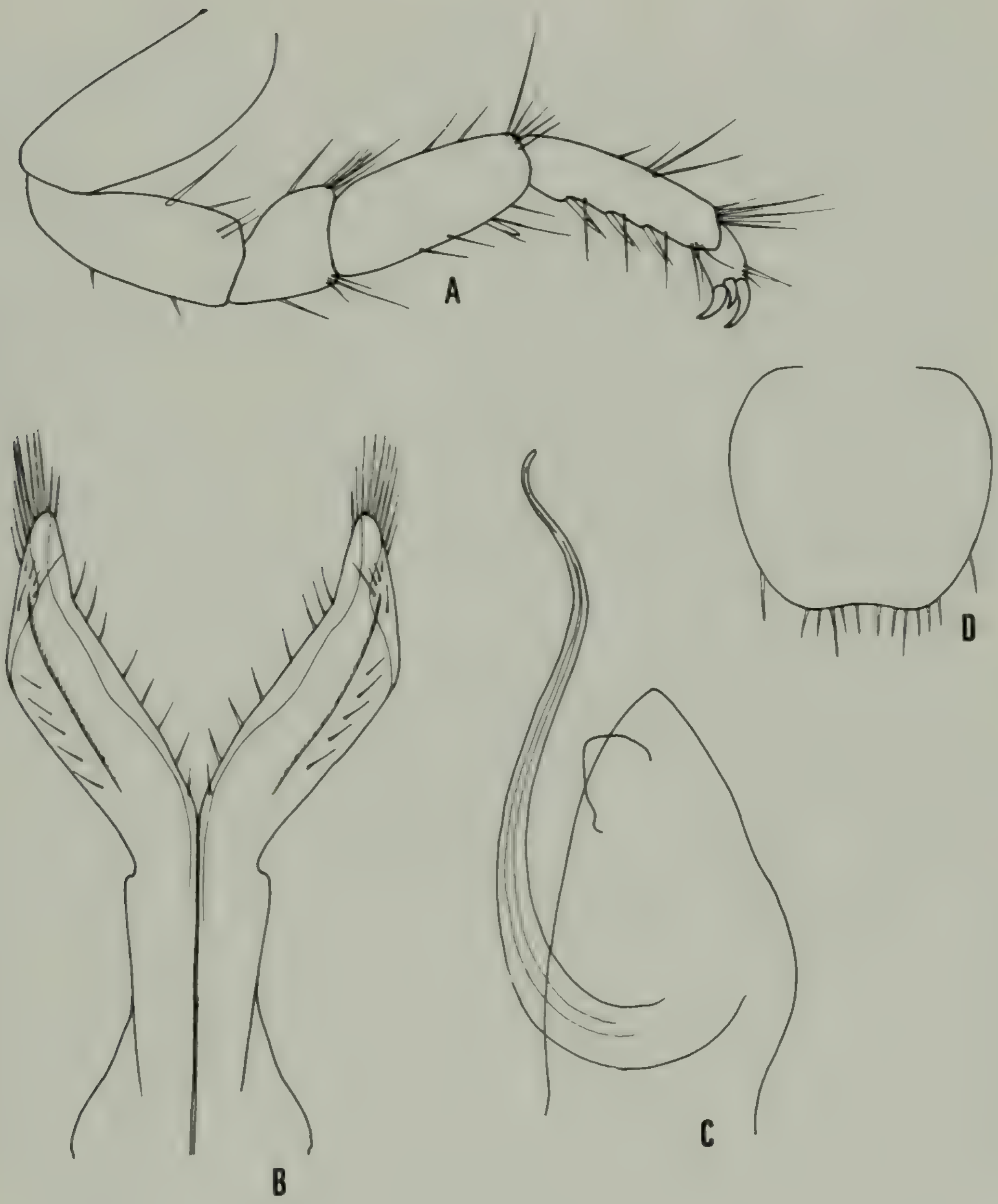

Fig. 16. *Ianiroides angusta* (Barnard).
A—Pereiopod VII; B—Pleopod 1 ♂; C—Pleopod 2 ♂; D—Operculum ♀.

Ianisera trepidus sp. nov.

Figs 17A–G, 18A–D

Description

Male: Body elongate, parallel-sided, bearing numerous short setae. Head anteriorly trilobed, rostral process evenly rounded; eyes tiny, dorsal, situated in posterior half of head. Coxal plates visible on all pereional segments. Pleotelson slightly longer than wide; lateral margins bearing about five serrations, posterior margin with broadly rounded median lobe; single lateral ridge on distal half, just median to lateral margin, ending distally in spine. Antennule about half length of antennae, consisting of large basal segment, second segment about half length and width of basal segment, flagellum of four segments. Antenna consisting of 5-segmented peduncle, second segment bearing well-developed scale; first and second segments equal in length to third segment, latter two-thirds length of fourth segment; flagellum of twelve segments. Mandible bearing 3-segmented palp, distal segment curved, armed with seven serrate spines, middle segment with four slender serrate spines; incisor process of five teeth, setal row of six serrate setae well separated from distally truncate molar process.

First maxilla, inner ramus bearing two stout setae plus several very fine setae, outer ramus with at least twelve serrate spines.

Second maxilla, outer ramus slender, bearing three elongate simple setae; outer lobe of inner ramus slender, bearing four elongate simple setae, inner ramus stout, carrying numerous simple setae.

Maxillipedal palp 5-segmented, two distal segments slender, three proximal segments expanded; endite bearing several fringed setae distally, two coupling hooks medially. Pereiopods similar, basal segment longest, all dactyli tipped with two curved spines. Pleopod 1 broad, two basal sections together forming almost complete sphere, distal area between median line and outer spine broadly convex, carrying about twenty alternately long and short setae.

Pleopod 2 bearing eight elongate simple setae distally.

Uropods with base almost hidden by distal margin of pleotelson, outer ramus slightly longer and broader than inner, both carrying numerous setae.

Female: Similar in all head and pereional appendages to male.

Operculum carrying numerous close-set setae on distal margin, latter somewhat concave medially.

Material

Holotype AMS 16.1.1971 1 ♂ 2;0 mm Paris Museum Is. 1007
Paratypes AMS 133 2 ♂♂ 1,1 mm 1,7 mm 2 ♀♀ 1,3 mm 1,9 mm Paris Museum Is. 1008
Paratypes AMS 17.1.1971 1 ♂ 1,8 mm 2 ♀♀ 1,3 mm 1,8 mm SAM–14996
AMS 39 2 ♀♀ 1,9 mm 2,0mm

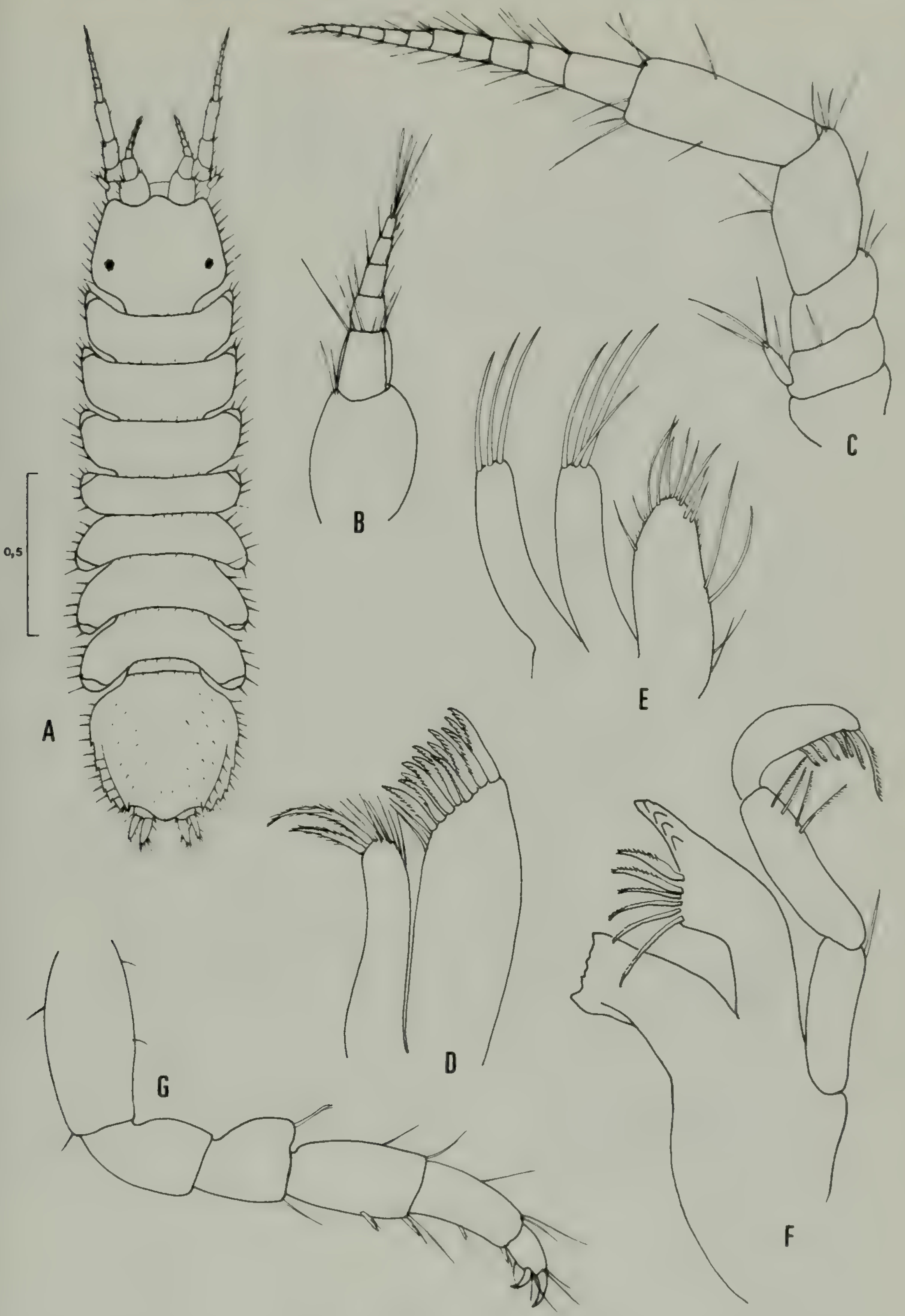

Fig. 17. *Ianisera trepidus* sp. nov.
A—Holotype in dorsal view; B—Antennule; C—Antenna; D—First maxilla; E—Second maxilla; F—Mandible; G—Pereiopod I.

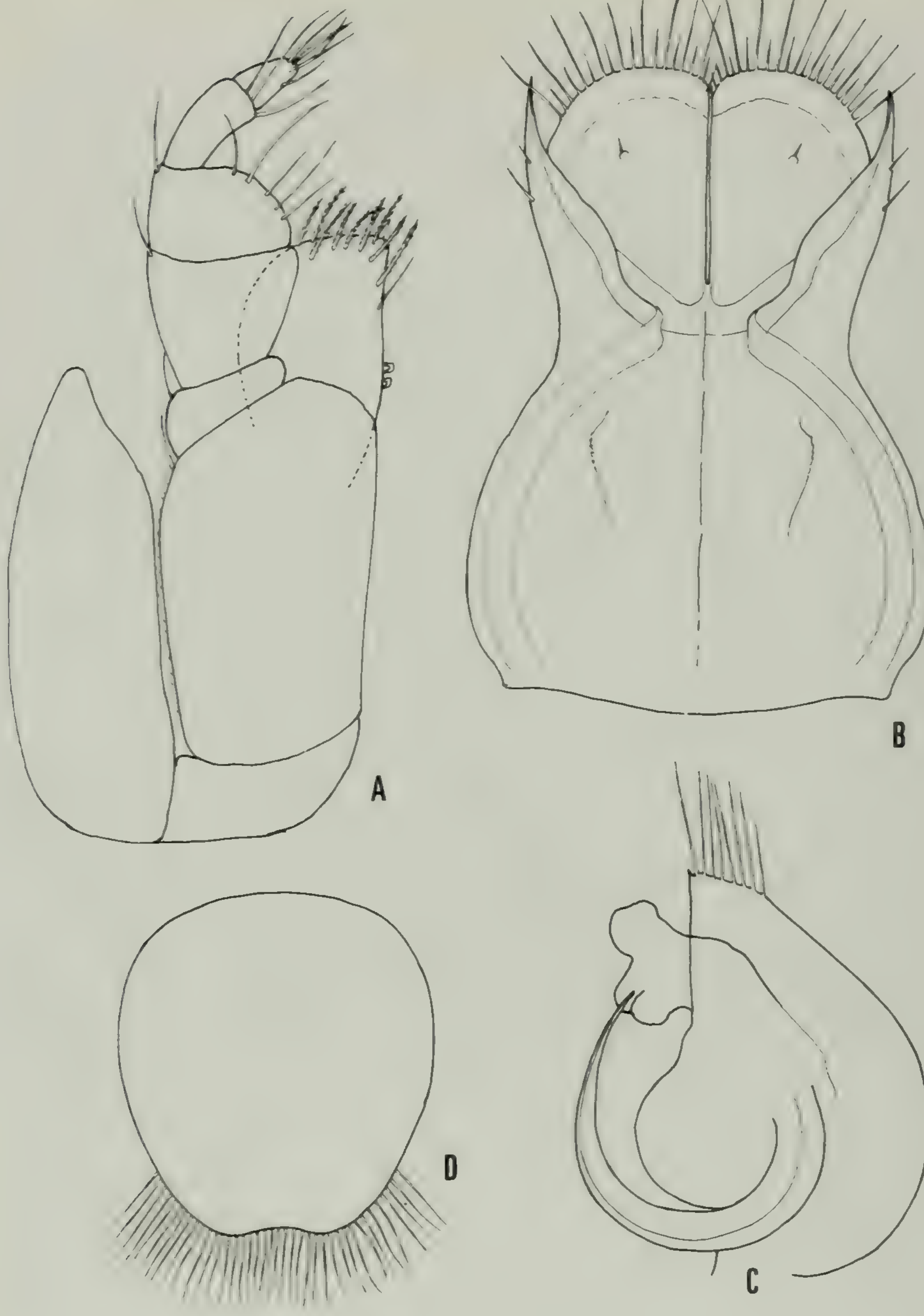

Fig. 18. *Ianisera trepidus* sp. nov.
A—Maxilliped; B—Pleopod 1 ♂; C—Pleopod 2 ♂; D—Operculum ♀.

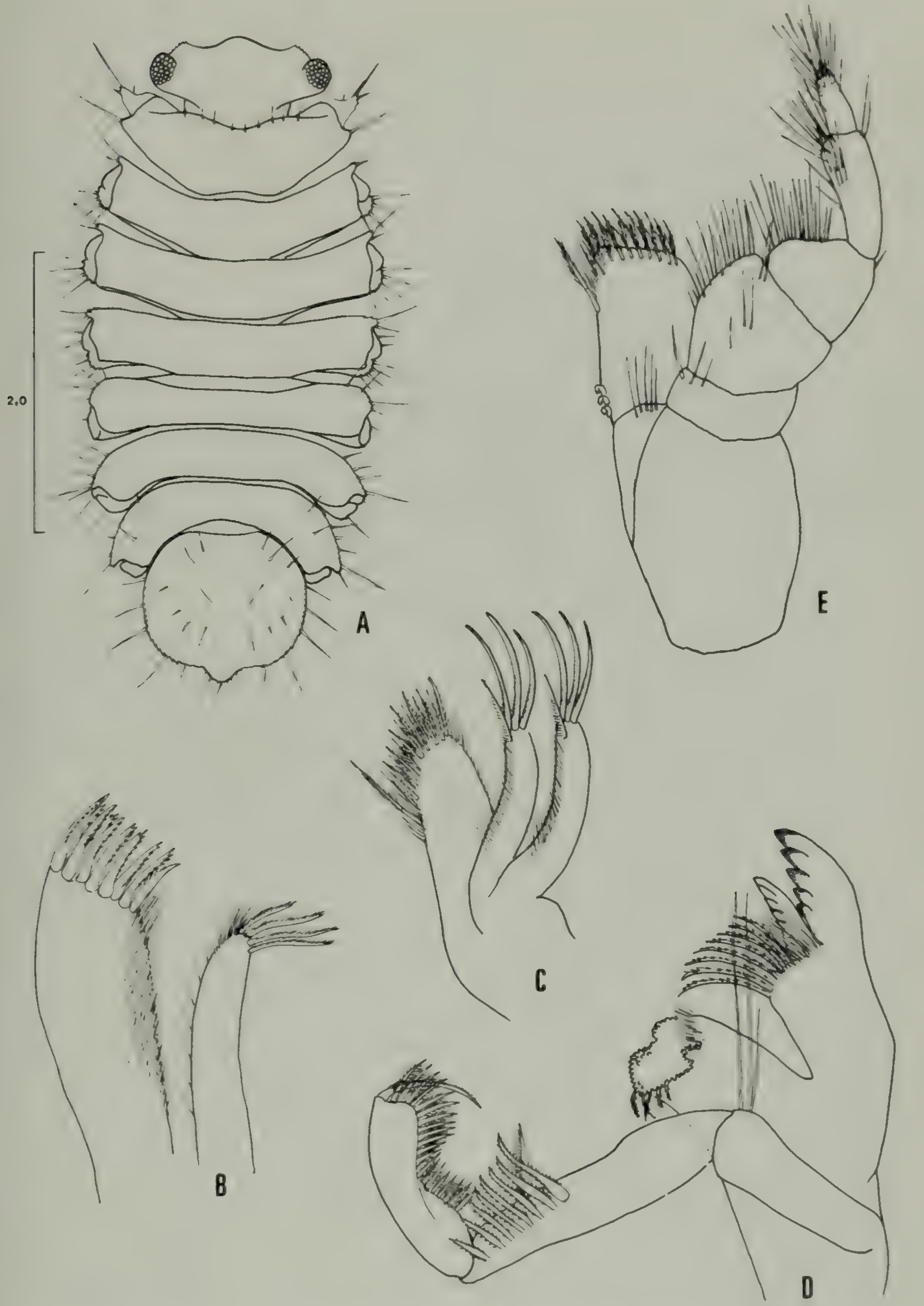

Fig. 19. *Janira capensis* Barnard.
A—♂ in dorsal view; B—First maxilla; C—Second maxilla; D—Mandible; E—Maxilliped.

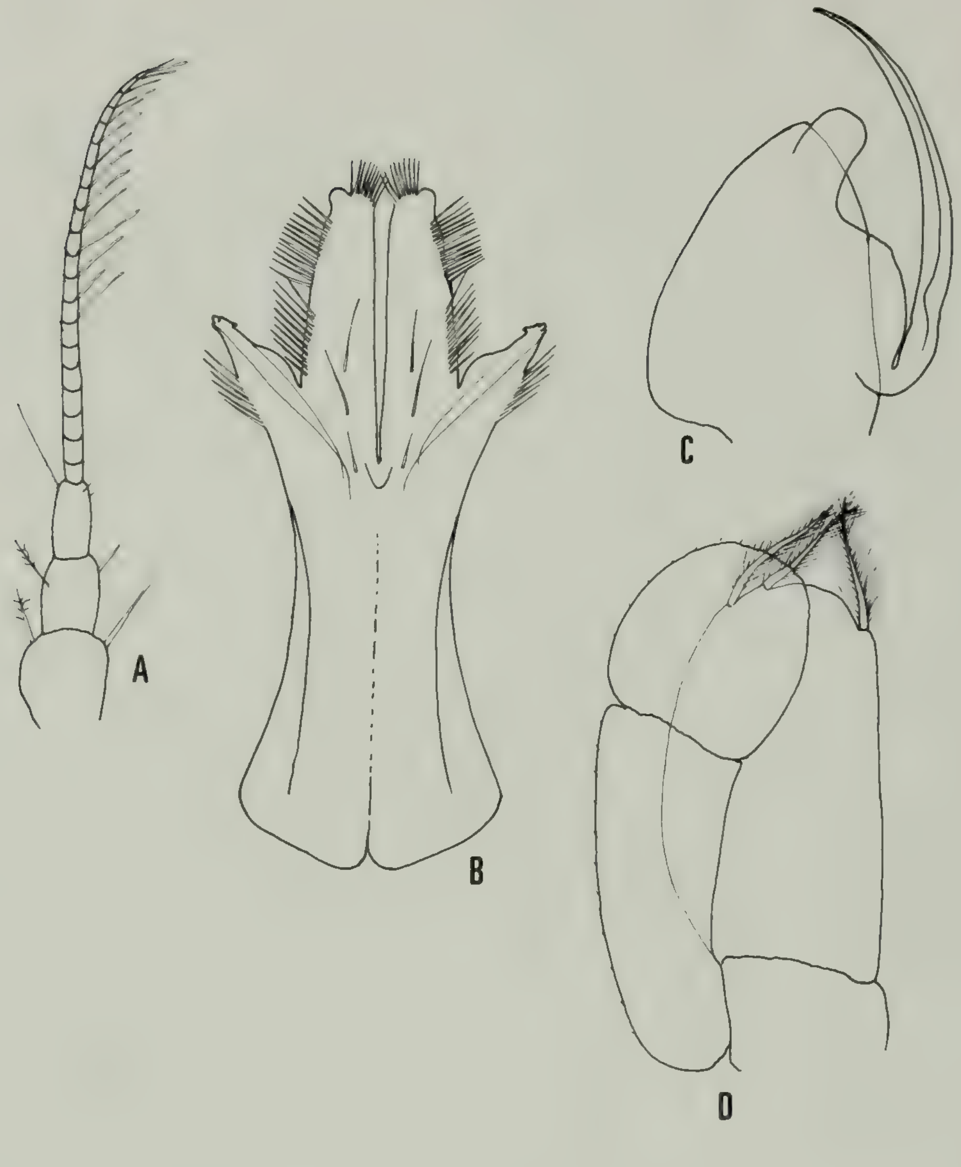

Fig. 20. *Janira capensis* Barnard.
A—Antenna; B—Pleopod 1 ♂; C—Pleopod 2 ♂; D—Pleopod 3 ♂.

Janira capensis Barnard

Figs 19A–E, 20A–D

Janira capensis Barnard, 1914: 220, pl. 20b. *non Iathrippa longicauda* Chilton, Menzies, 1962: 72.

Previous records

Lüderitzbucht, Saldanha Bay, Table Bay, False Bay.

Material

AMS	a7	
	24a	1 ♂

St Paul	6c	2 ♂♂	2 ♀♀		
	7a	3 ♂♂	2 ♀♀		
	B7	3 ♂♂	1 ♀ 1 juv.		
	7b	12 ♂♂	3 ovig. ♀♀	4 ♀♀	
	18	13 ♂♂	2 ovig. ♀♀	11 ♀♀	
	20	4 ♂♂		3 ♀♀	
	22a	5 ♂♂	1 ovig. ♀	2 ♀♀	
	22c	7 ♂♂	7 ovig. ♀♀	10 ♀♀	4 juv.
	23	5 ♂♂	1 ovig. ♀	8 ♀♀	8 juv.
	30a	1 ♂		1 ♀	
	30b	2 ♂♂		1 ♀	
	32	1 ♂			
	91	7 ♂♂	2 ovig. ♀♀	3 ♀♀	

Remarks

Nordenstam (1933), in his description of *I. longicauda*, figures the pleotelsonic margins entire, the carpus of pereiopod I without a distal curved spine, and mentions the distinct rostrum for the species. Menzies (1962, fig. 51f–g) also shows a well-developed rostrum, which is lacking in the present material. Thus *I. longicauda* is easily distinguishable from Barnard's valid species.

Ianiropsis palpalis Barnard

Fig. 21

Ianiropsis palpalis Barnard, 1914: 222, pl. 21A. Wolff, 1962: 251.

Previous records

Lüderitzbucht, Table Bay, False Bay, Port Elizabeth, East London.

Material

AMS			
A6		1 ♀	
B9		1 ♀	
b1	6 ♂♂	3 ♀♀	3 ovig. ♀♀
b3	20 ♂♂	11 ♀♀	7 ovig. ♀♀
D1	2 ♂♂	4 ♀♀	
D7		1 ♀	
D9	10 ♂♂	10 ♀♀	11 ovig. ♀♀
D12	11 ♂♂	8 ♀♀	7 ovig. ♀♀
J11	1 ♂	2 ♀♀	
P1	4 ♂♂		
P4	1 ♂		
P19	1 ♂	2 ♀♀	1 ovig. ♀
P28		1 ♀	
P34		1 ♀	
P45			1 ovig. ♀
P83	1 ♂		
27.3.1970/b	1 ♂	3 ♀♀	
28.3.1970/b	2 ♂♂	2 ♀♀	
12.12.1970	2 ♂♂	1 ♀	1 ovig. ♀
17.1.1971		3 ♀♀	1 ovig. ♀
16.1.1971	4 ♂♂	1 ♀	
4		1 ♀	

St Paul			
B7	2 ♂♂	2 ♀♀	1 ovig. ♀
B19	9 ♂♂	6 ♀♀	
D3	4 ♂♂	1 ♀	
D5/a	1 ♂	3 ♀♀	1 ovig. ♀
D5/c	3 ♂♂	2 ♀♀	4 ovig. ♀♀
D6	20 ♂♂	4 ♀♀	5 ovig. ♀♀
D8	1 ♂		
D11	1 ♂		
3	40 ♂♂	22 ♀♀	15 ovig. ♀♀
7a	10 ♂♂	7 ♀♀	11 ovig. ♀♀
7b	8 ♂♂	6 ♀♀	7 ovig. ♀♀
14			2 ovig. ♀♀
16	2 ♂♂	1 ♀	1 ovig. ♀
18	14 ♂♂	3 ♀♀	3 ovig. ♀♀
19	2 ♂♂	1 ♀	1 ovig. ♀
20	20 ♂♂	9 ♀♀	13 ovig. ♀♀
22a	8 ♂♂	2 ♀♀	6 ovig. ♀♀
22b	6 ♂♂	2 ♀♀	3 ovig. ♀♀
22c	12 ♂♂	7 ♀♀	1 ovig. ♀
23	5 ♂♂	2 ♀♀	3 ovig. ♀♀
23a	1 ♂	1 ♀	2 ovig. ♀♀
24b			2 ovig. ♀♀

Material

9	1 ♂		
11	1 ♂	1 ♀	
14	22 ♂♂	34 ♀♀	4 ovig. ♀♀
28	52 ♂♂	52 ♀♀	25 ovig. ♀♀
39	17 ♂♂	6 ♀♀	4 ovig. ♀♀
41a	30 ♂♂	22 ♀♀	11 ovig. ♀♀
41b	1 ♂	3 ♀♀	2 ovig. ♀♀
48	28 ♂♂	29 ♀♀	4 ovig. ♀♀
60	8 ♂♂	4 ♀♀	2 ovig. ♀♀
64a	29 ♂♂	9 ♀♀	12 ovig. ♀♀
64b	2 ♂♂	3 ♀♀	2 ovig. ♀♀
73	5 ♂♂	7 ♀♀	3 ovig. ♀♀
74	8 ♂♂	4 ♀♀	
83	2 ♂♂		1 ovig. ♀
94	66 ♂♂	30 ♀♀	31 ovig. ♀♀
96	42 ♂♂	20 ♀♀	11 ovig. ♀♀
101	5 ♂♂	5 ♀♀	5 ovig. ♀♀
103	18 ♂♂	9 ♀♀	4 ovig. ♀♀
111			1 ovig. ♀
119	16 ♂♂	6 ♀♀	6 ovig. ♀♀
132	2 ♂♂	3 ♀♀	
133	4 ♂♂	1 ♀	1 ovig. ♀
142b	21 ♂♂	10 ♀♀	2 ovig. ♀♀
147	2 ♂♂	2 ♀♀	
148	4 ♂♂	4 ♀♀	
166	58 ♂♂	40 ♀♀	34 ovig. ♀♀
173	75 ♂♂	34 ♀♀	44 ovig. ♀♀

30a	8 ♂♂	5 ♀♀	3 ovig. ♀♀
30b	26 ♂♂	12 ♀♀	8 ovig. ♀♀
35	21 ♂♂	15 ♀♀	11 ovig. ♀♀
67	1 ♂		
77a	6 ♂♂	3 ♀♀	3 ovig. ♀♀
90	5 ♂♂		3 ovig. ♀♀
1970		1 ♀	1 ovig. ♀
91	2 ♂♂	1 ♀	1 ovig. ♀
1.1971	2 ♂♂	3 ♀♀	4 ovig. ♀♀
29.1.1971	36 ♂♂	11 ♀♀	11 ovig. ♀♀

Family **Jaeropsidae**

Jaeropsis beuroisi Kensley

Jaeropsis beuroisi Kensley, 1975: 374, figs 7–8.

Previous records

St Paul and Amsterdam Islands.

Material

AMS			
D12	2 ♂♂	1 ♀	1 ovig. ♀
39		1 ♀	1 ovig. ♀
41a	1 ♂	1 ♀	
41b	1 ♂		
44		1 ♀	
64a	1 ♂		1 ovig. ♀
74	4 ♂♂		
94	2 ♂♂		
119	11 ♂♂	8 ♀♀	2 ovig. ♀♀
142b	2 ♂♂	3 ♀♀	2 ovig. ♀♀
147	1 ♂	1 ♀	
173	6 ♂♂	6 ♀♀	4 ovig. ♀♀

St Paul			
B7		1 ♀	
B19	1 ♂	1 ♀	
D6	5 ♂♂	2 ♀♀	1 ovig. ♀
3	1 ♂	2 ♀♀	
7b	13 ♂♂	13 ♀♀	10 ovig. ♀♀
18	5 ♂♂	3 ♀♀	4 ovig. ♀♀
20	1 ♂	1 ♀	1 ovig. ♀
22c	12 ♂♂	2 ♀♀	9 ovig. ♀♀
77a	4 ♂♂	1 ♀	1 ovig. ♀
90	18 ♂♂	20 ♀♀	
29.12.1970			1 juv.
19.1.1971		1 ♀	

Jaeropsis paulensis Vanhöffen

Jaeropsis paulensis Vanhöffen, 1914: 531, fig. 59a. Barnard, 1965: 201, fig. 2b. Kensley, 1975: 371, figs 5–6.

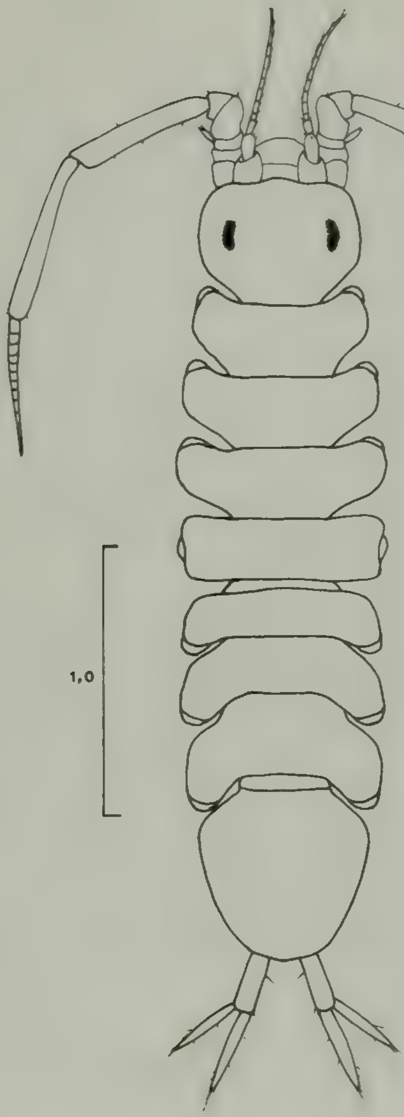

Fig. 21. *Ianiropsis palpalis* Barnard.
♂ in dorsal view.

Previous records

St Paul Island, Gough Island.

Material

AMS			
a4	9 ♂♂		8 ovig. ♀♀
a8		2 ♀♀	
a9	1 ♂		
b3	3 ♂♂	6 ♀♀	3 ovig. ♀♀
14	2 ♂♂	2 ♀♀	1 ovig. ♀
27.3.1970/b	1 ♂		

St Paul			
8a	14 ♂♂	5 ♀♀	1 ovig. ♀
8b	3 ♂♂	1 ♀	2 ovig. ♀♀
8c	9 ♂♂	3 ♀♀	2 ovig. ♀♀
93	7 ♂♂	2 ♀♀	4 ovig. ♀♀

Family **Munnidae**

Munnogonium subtilis sp. nov.

Fig. 22A–I

Description

Female: Body pear-shaped, widest at second and third pereional segments. Head with anterior margin between antennules straight; eyestalks elongate. Pereional segments I–IV broad, antero-lateral corners of segment I rounded, of segment II quadrate, segments III and IV notched; segments V to VII narrower than preceding segments, with coxal plates visible. Pleotelson as long as broad, distally broadly rounded, lateral margins as far as insertion of uropoda dentate (about 12 teeth). Antennule with 2-segmented peduncle, basal segment shorter, more curved and wider than second segment; flagellum 4-segmented. Antennae missing.

Mandible with narrow toothed incisor process, narrow lacinia mobilis, followed by four elongate setae; molar process elongate, distally slightly expanded, truncate; palp missing.

Maxilliped with two distal segments of palp much narrower than three proximal segments; endite bearing about 6 setae (three simple, three plumose), plus two coupling hooks. Pereiopod I dactylus bearing elongate terminal curved spine plus smaller spine; propodus with two sensory spines on ventral margin, carpus somewhat shorter and broader than propodus, also with two sensory spines on ventral margin; basis elongate, equal in length to merus and ischium.

Operculum distally narrowed to rounded apex bearing four stout setae.

Uropoda short, biramous, inner ramus half length and width of outer.

Material

Holotype	AMS D9	1 ovig. ♀	total length 1,8 mm	Paris Museum Is. 1009

Remarks

Bowman & Schultz (1974) recently revised the genus *Munnogonium* George & Stromberg. They separated the members of the genus from the closely related species of *Austrosignum* Nordenstam by the lack of a mandibular palp in species of *Munnogonium*. The resemblance is most marked in general body shape and proportion between the new species and *A. latifrons* Menzies (1962), but that species has a palp on the mandible. *A. globifrons* Menzies was placed in *Munnogonium* by Bowman and Schultz, but does not resemble the new species as closely in general body shape as does *A. latifrons*. The new species also resembles *Paramunna kerguelensis* Vanhöffen, but it is not known if a mandibular palp is present or absent in this species.

Genus *Coulmannia* Hodgson

Hodgson, 1910: 52. Vanhöffen, 1914: 580. Nordenstam, 1933: 225. Menzies, 1962: 173. Wolff, 1962: 62.

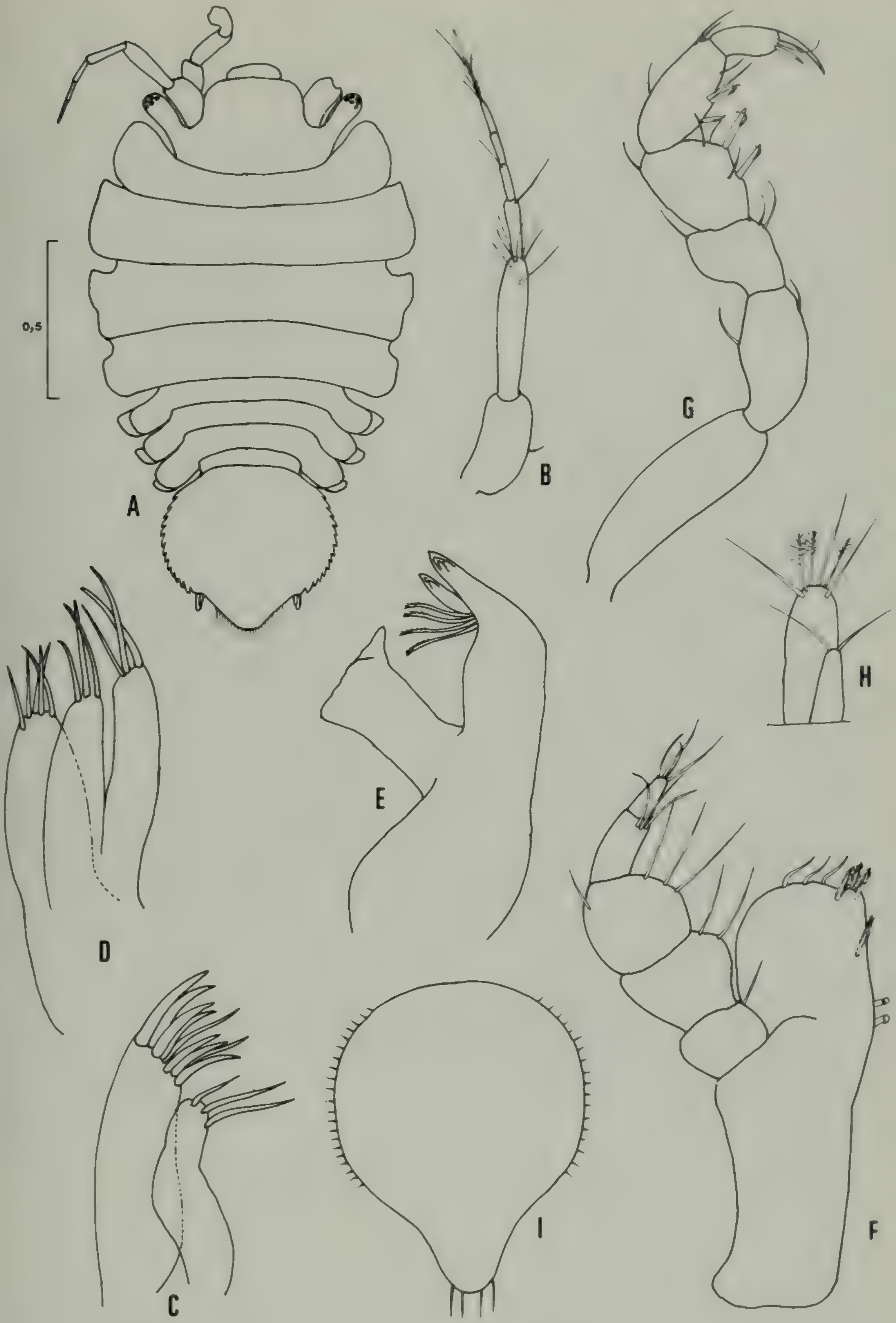

Fig. 22. *Munnogonium subtilis* sp. nov.
A – Holotype in dorsal view; B – Antennule; C – First maxilla; D – Second maxilla; E – Mandible; F – Maxilliped; G – Pereiopod I; H – Uropoda; I – Operculum.

Coulmannia unicornis sp. nov.

Figs 23A–F, 24A–H

Description

Male: Head steeply rounded anteriorly. Pereion widest at IIIrd segment. Pereional segment I laterally bulbous, rounded, bearing strong medio-dorsal 'horn', segments II–IV each with single digitiform lateral extension; segments V–VII posteriorly directed, laterally rounded. Pleotelson anteriorly narrow, cylindrical, posteriorly bulbous, with five serrations on each side, apically bluntly rounded.

Eyestalks reaching to proximal half of second antennular segment, with four ocelli. Antennule with two subequal peduncular segments, flagellum of four segments. Antenna with 5-segmented peduncle, two distal segments elongate, subequal; flagellum of six segments.

Mandible lacking palp, with incisor process bearing five teeth; setal row of three setae; molar process large, cylindrical, distally truncate, with blunt irregular teeth on grinding surface.

Maxillipedal palp 5-segmented, three basal segments broad, two distal segments more slender, all segments bearing setae; endite with strong conical tooth at medio-distal corner, seven or eight setae, single coupling hook present.

Pereiopod I subchelate, carpus with emarginate fringed palm, demarked by strong conical tooth; dactylus with long unguis; propodus bearing two stout setae with sensory tips.

Pereiopods II–VII similar, longer and more slender than pereiopod I; dactyli with long unguis; propodi and carpi elongate, meri short, ischium and bases subequal elongate. Pleopod 1 proximally fused, distally separate, distal lobes triangular, with outer basal corners bearing several short setae.

Uropod biramous, inserted without peduncle beneath ridge on bulbous pleotelson; endopod half length of exopod, both tipped with elongate setae.

Female: Pereional segments II–IV broader than in male; pereional segment I not armed with 'horn' as in male.

Pereiopod I shorter than following legs, but not subchelate.

Operculum longer than broad, distally tapering to bluntly rounded tip, fringed at widest part with short setae.

Material

Holotype	AMS 17.1.1971.	1 ♂	2,0 mm	Paris Museum Is. 1010
Allotype	AMS 17.1.1971.	1 ovig. ♀	1,4 mm	Paris Museum Is. 1011

Remarks

The absence of a mandibular palp is the most important character of this genus, along with the strong apically truncate molar process of the mandible.

Hodgson created the genus for two species, viz. *C. australis* from Coulman Island in Victoria Land, South Georgia, and Graham Land, and *C. frigida*, described from a single specimen also from the Antarctic. The differences

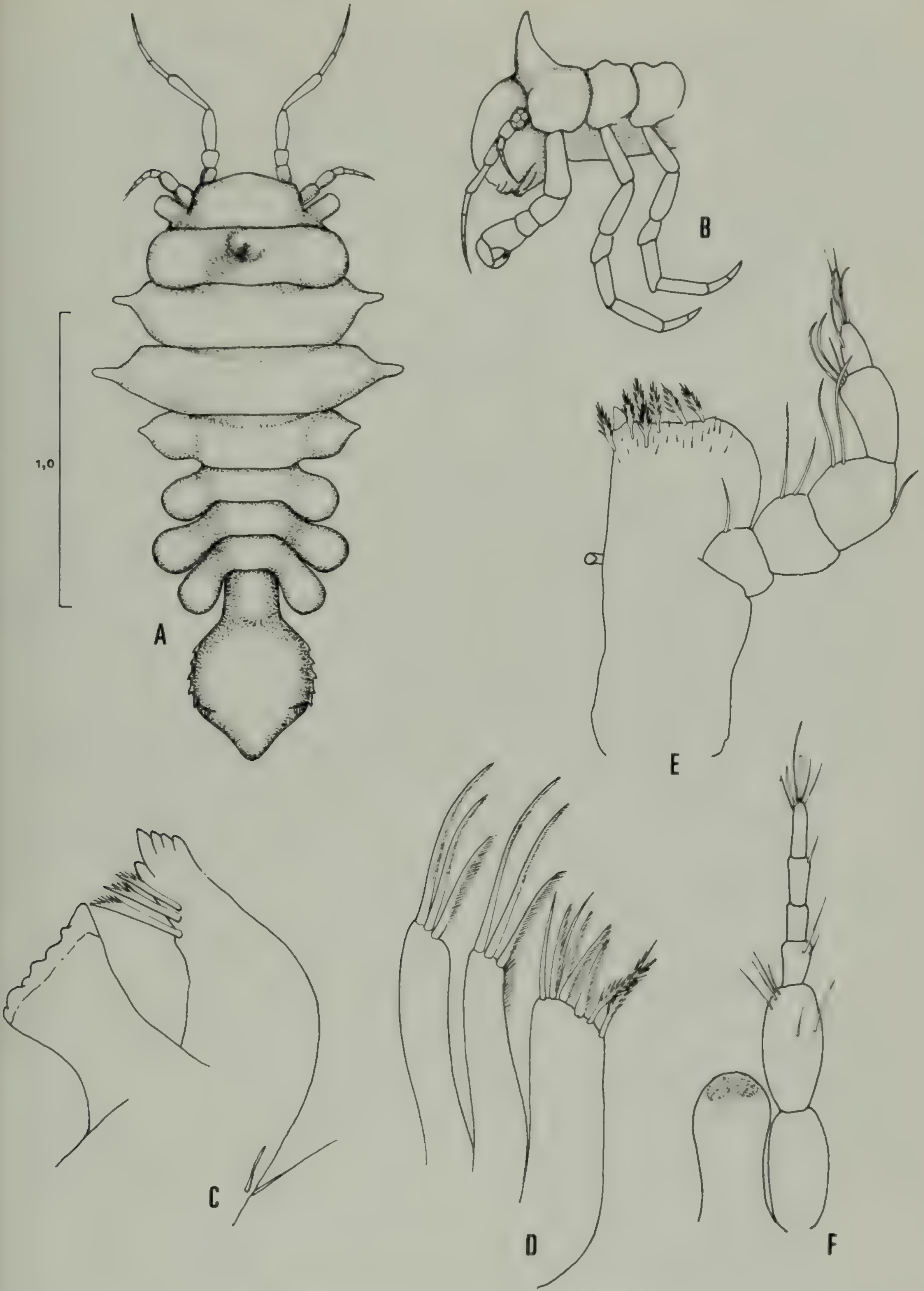

Fig. 23. *Coulmannia unicornis* sp. nov.
A—Holotype in dorsal view; B—Head and anterior segments in lateral view; C—Mandible; D—Second maxilla; E—Maxilliped; F—Antennule and eyestalk.

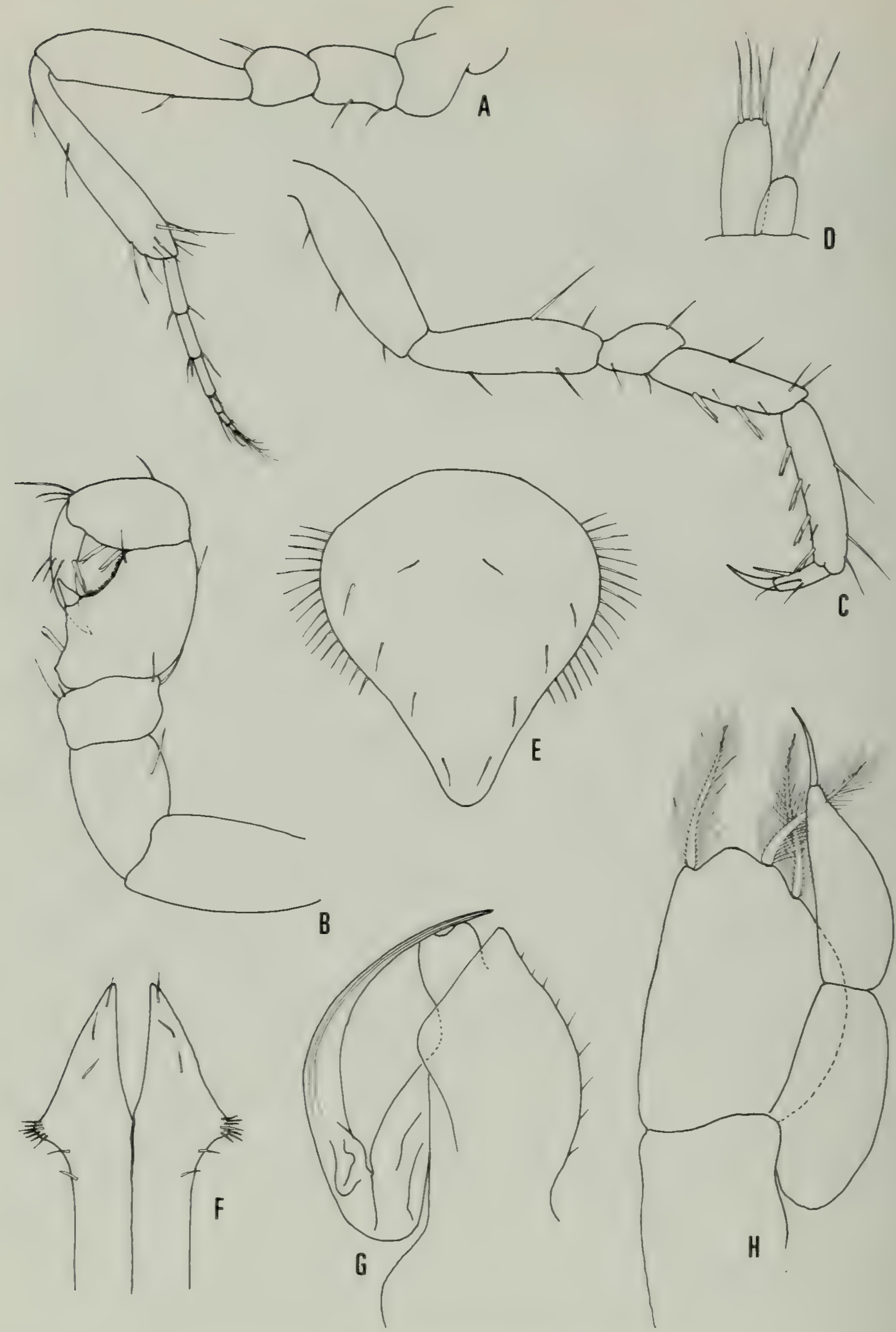

Fig. 24. *Coulmannia unicornis* sp. nov.
A—Antenna; B—Pereiopod I; C—Pereiopod VII; D—Uropoda; E—Operculum ♀; F—Pleopod 1 ♂; G—Pleopod 2 ♂; H—Pleopod 3 ♂.

between these two species and *C. unicornis* are readily apparent. The most obvious is in the structure of the lateral pereional extensions—bifid in *C. australis*, single in *C. unicornis* and *C. frigida. C. australis* carries a single median dorsal spine on each of the pereional segments while in the present species, only the first pereional segment bears a strong dorsal 'horn' (hence the specific name). Regarding the appendages, there is general agreement between those of *C. australis*, well illustrated by Nordenstam (1933) and the present species. Subtle differences are apparent, particularly in the maxilliped, and first pereiopod of the male.

Echinomunna uroventralis sp. nov.

Figs 25A–E, 26A–D

Description

Female: Body longer than wide, spinose. Head bearing three spines anteriorly, median spine at higher level than lateral spines. Eyes lateral. Pereional segments each bearing strong lateral spine, with two coxal spines visible in dorsal view. Pereional segment I with two submedian dorsal spines, segments II–IV with seven dorsal spines, segments V–VII with three dorsal spines. Pleon fused, longer than wide, with two strong backwardly-directed lateral spines at widest point, medio-distally with two long diverging spines.

Antennule with 2-segmented peduncle, segments subequal in length, basal segment wider than distal segment; flagellum 4-segmented, two proximal and distal segment subequal, short, third segment nine times longer than wide, very slender. Antennae in all specimens with flagella missing; peduncle of four short segments, second and third segments each with two strong spines.

Right mandible, incisor process of five strong teeth, followed by five strong fringed setae, molar process strong, distally truncate; palp 3-segmented, basal segment two-thirds length of middle segment, distal segment curved, half length of middle segment, bearing two or three fringed setae, plus numerous fine setules. Left mandible with incisor process of five strong teeth, narrow lacinia mobilis carrying five teeth, four stout fringed setae in setal row.

Maxillipedal endite broad, with nine or ten short setae on medio-distal margin, three coupling hooks on median margin, palp 6-segmented, with first to third segments wider than fourth to sixth segments, but not as marked as in *Echinomunna* s.s., first segment one-third length of second segment, third segment somewhat shorter than second, segments four and five subequal in length, terminal segment tiny.

Pereiopod I considerably shorter than following pereiopods; dactylus curved, with well-marked unguis; propodus with convex palm bearing delicate fringed membrane plus several stout setae with sensory tips; carpus distally broader than proximally, shorter than propodus, subequal to merus in length; ischium and basis elongate, subequal.

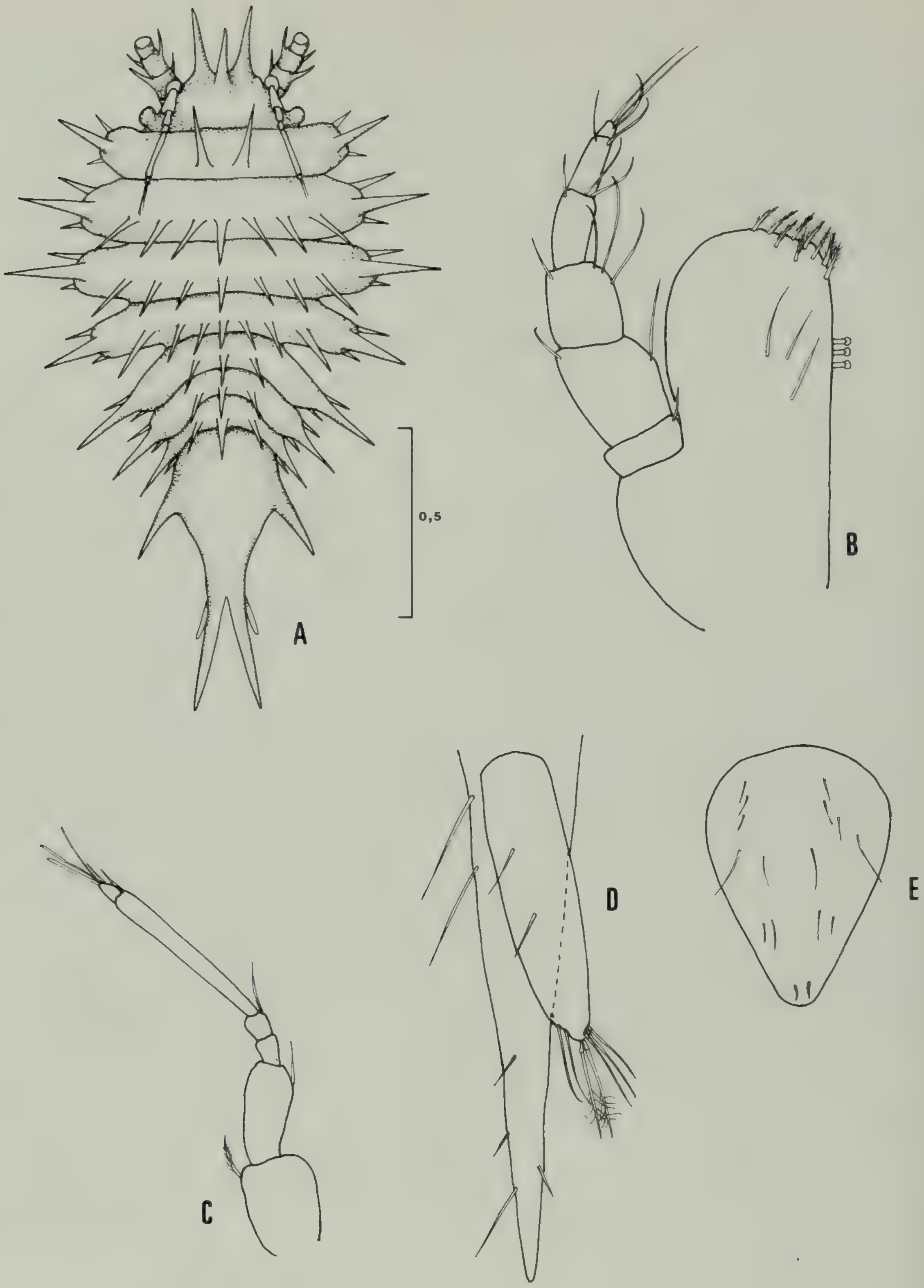

Fig. 25. *Echinomunna uroventralis* sp. nov.
A—Holotype in dorsal view; B—Maxilliped; C—Antennule; D—Uropod; E—Operculum ♀

Pereiopods II–VII slender, elongate, dactyli bearing two terminal claws; propodi and carpi slender, elongate; meri, ischia, and bases much shorter, coxae carrying two or three spinose processes, visible dorsally beneath lateral pereional spine.

Operculum longer than wide, distally tapering to broadly-rounded apex.

Uropods ventral to posterior pleonal spines, uniramous, tipped with several setae, three-and-a-half times longer than wide.

Material

Holotype	AMS 28	1 ovig. ♀	Total length 1,8 mm	Paris Museum Is. 1012
Paratypes	AMS 28	2 ovig. ♀♀	Total length 1,7 mm	Paris Museum Is. 1013

Remarks

The slender ambulatory pereiopods, lateral eyes, the pleon longer than broad, segments one to three of the maxillipedal palp broader than segments four to six, the uropod lacking a peduncle, the strong mandibular molar process, apically truncate, all place this species in the family Munnidae. Nevertheless, some differences are apparent when considering the various diagnoses for the family (e.g. Menzies 1962: 172; Wolff 1962: 59–60). The first three segments of the maxillipedal palp are not as wide as the endite, and a second pleonal segment is not visible.

A generic position for this species cannot be arrived at with any confidence. From Menzies's key (1962), using the following characters, one arrives at the choice of either *Echinomunna* or *Acanthomunna*: coxal plates visible in dorsal view, mandibular palp 3-segmented, coxal plates visible on pereional segments two to seven, body strongly spinose. The uropods of the present species are neither lateral as in *Echinomunna* nor dorsal as in *Acanthomunna*. The relatively massive, pedunculate, biramous uropods of *Acanthomunna* would seem to rule out this genus. Using Wolff's key (1962), the following characters place the species in the genus *Echinomunna*: molar process subcylindrical and strong, coxal plates two to seven visible in dorsal view, body strongly spinose.

The present material agrees with Vanhöffen's description of *Echinomunna horrida* in the spinose body, the position of the eyes, the construction of the antennule with one long flagellar segment plus several short segments, in the structure of the maxilliped and the first pereiopod. The main differences between *E. horrida* and *E. uroventralis* lie in the number of dorsal pereional spines, and especially in the pleonal structure with the ventrally inserted uropods. The Antarctic species possesses five proximal spines, while the uropods are inserted laterally, and the pleon is distally rounded-truncate. In *E. uroventralis* there are two strong lateral spines, plus two submedian distal spines with the uropods inserted beneath them.

The present species is thus placed in the genus *Echinomunna* with some reservations, and with the necessity to enlarge the definition of the genus to include uropods which are inserted either laterally or ventrally.

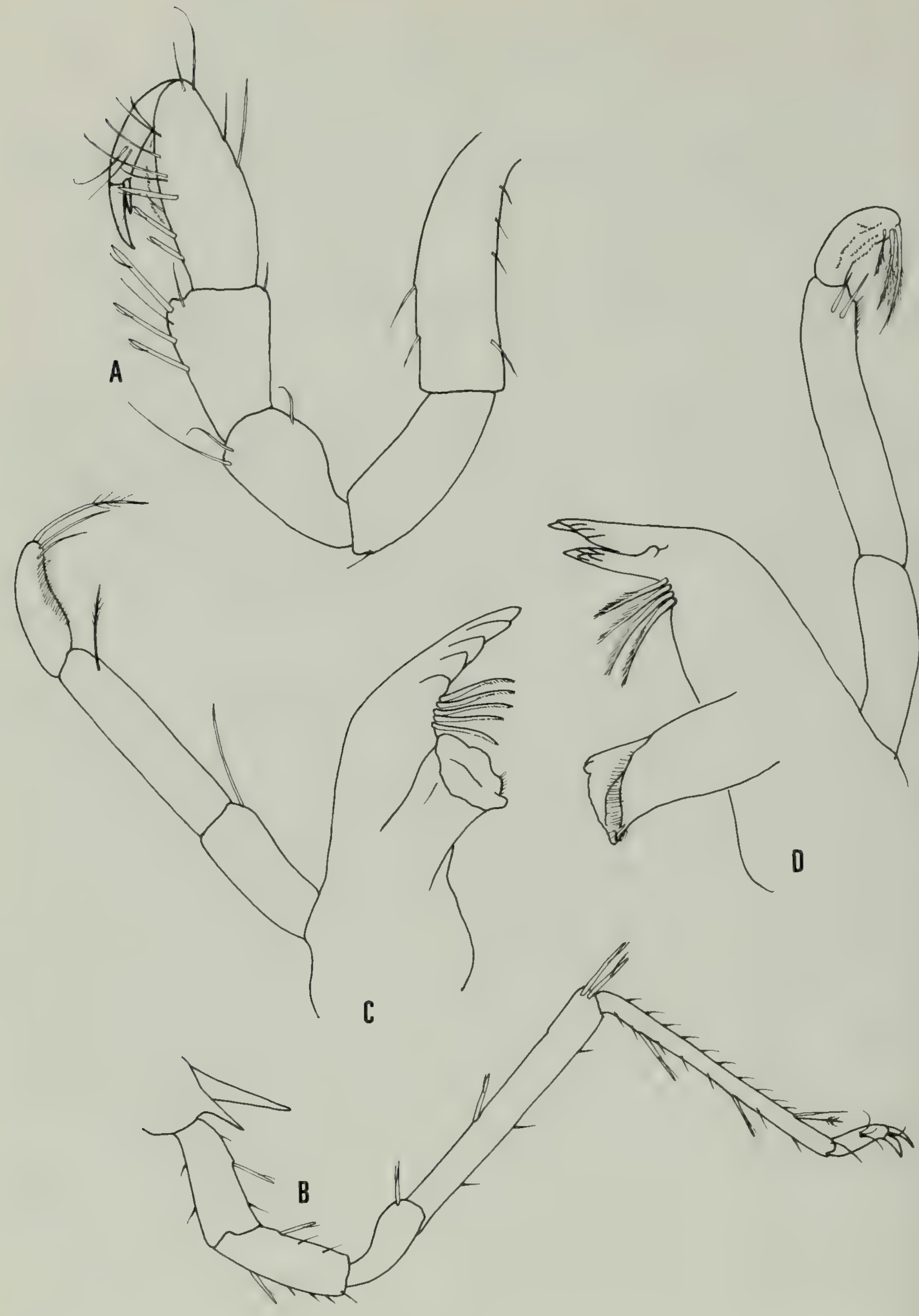

Fig. 26. *Echinomunna uroventralis* sp. nov.
A—Pereiopod I; B—Pereiopod VII; C—Right mandible; D—Left mandible.

Munna (*Uromunna*) *nana* Nordenstam

Munna nana Nordenstam, 1933: 222, figs. 56–57.
Munna nana forma "a" Menzies, 1962: 42 fig 5.

Previous records

Chile, Falkland Islands.

Material

AMS	a4		2 ♀♀		St Paul	B19		1 ♀	1 ovig. ♀
	C1			1 ovig. ♀		D36	1 ♂		1 ovig. ♀
	28		2 ♀♀	4 ovig. ♀♀		6c	2 ♂♂		
	41a	1 ♂		2 ovig. ♀♀		7a	3 ♂♂	2 ♀♀	2 ovig. ♀♀
	48			1 ovig. ♀		8c			1 ovig. ♀
	64a	1 ♂				19	1 ♂		2 ovig. ♀♀
	94		1 ♀			22a		1 ♀	
	96			2 ovig ♀♀		22c	2 ♂♂	3 ♀♀	3 ovig. ♀♀
	103		1 ♀			23a			1 ovig. ♀
	142b	3 ♂♂		1 ovig. ♀		30a			1 ovig. ♀
	173		1 ♀			30b		1 ♀	1 ovig. ♀
						77a	1 ♂	1 ♀	
						77b			1 ovig. ♀
						90	5 ♂♂	10 ♀♀	2 ovig. ♀♀

Remarks

Slight differences between the present material and Menzies's forma 'a' as well as the forma typica are apparent. The last segment of the antennal peduncle is not twice the length of the penultimate segment, while the superior dactylar spine of the pereiopods is smooth.

Suborder Oniscoidea

Family **Oniscidae**

Subfamily Scyphacinae

Deto echinata Guérin

Deto echinata: Budde-Lund, 1885: 234; 1906: 85, pl. 4 (figs 37–38). Panning, 1924: 185, figs 4–8. Barnard, 1932: 221, fig. 12. Vandel, 1945: 261. Green, 1974: 240.
Deto armata Budde-Lund, 1906: 85, pl. 4 (figs 26–36). Panning, 1924: 191, fig. 10.

Previous records

Rocky Point (S.W.A.), Lüderitzbucht, Lamberts Bay, Olifants River Mouth, Dyers Island, Dassen Island, Table Bay, False Bay, Hermanus, Knysna, St Paul Island.

Material

AMS	a6	7 ♂♂	4 ♀♀
	15	32 ♂♂	26 ♀♀
	27.3.1970/a		2 ♀♀
	28.3.1970/a	24 ♂♂	18 ♀♀

Remarks

Panning (1924) synonymized *D. armata* with *D. acinosa*, which he regarded as a species separate from *D. echinata*. His figure 10, however, is of an immature male from St Paul Island, not yet showing the development of dorsal spines on pereion and pleon. Barnard (1932) regards *D. acinosa* (and with it *D. armata*) as synonymous with *D. echinata*, but qualifies this by stating that the small strongly granulate form of *D. echinata* might be regarded as the form *acinosa*.

That this group of isopods is extremely variable is without doubt. It is interesting, however, to note the following: of about 100 mature males of *D. echinata* from South African localities examined, none showed spinose processes on the pleon, and that both mature males and females from South Africa frequently reach a total length of more than 20 mm. Of the 64 adult males from St Paul and Amsterdam Islands examined, none were larger than 17,5 mm; while 42 specimens possessed a pair of spines on the third pleonal segment, 14 showed a pair of spines on both pleonal segments three and four, while 8 specimens lacked pleonal spines completely. Further, these pereional and pleonal spines never showed the markedly incurved condition of the South African forms. No differences in the structure of the male genital apparatus could be seen between St Paul–Amsterdam Island specimens and South African specimens. It would seem that the St Paul–Amsterdam Island population should be regarded as part of the *D. echinata* group, but that this island population, isolated as it is, is beginning to show morphological signs of diverging from the mainland African stock.

Family **Oniscidae**

Porcellio scaber Latreille

Porcellio scaber: Budde-Lund, 1906: 88. Barnard, 1932: 252, fig. 21 (references).
Porcellio paulensis Heller, 1865: 136, pl. 12 (fig. 5). Brocchi, 1877: 97. André, 1932: 177, 180.

Previous records

Cape Province, St Helena Island, Tristan da Cunha, St Paul and Amsterdam Islands.

Material

AMS	5a	1 ovig. ♀	2 juv.
	6a	6 ♀♀	
	6b	1 juv.	

ZOOGEOGRAPHICAL DISCUSSION

The total number of species of isopods from the St Paul and Amsterdam Islands, including past collections plus the present collection, is 43. To get the effective list of species on which zoogeographical conclusions may be based, the two undetermined species, viz. *Munna* sp., and the damaged tanaid, and the four inadequately described species of Brocchi (1877) the types of which have been lost, viz. *Spheroma* (*sic*) *tuberculata*, *Cymodoce picta*, *Cymothoa gadorum*, and *Rocinela major*, must be removed. This leaves an effective total of thirty-seven species. These thirty-seven species may be divided into various categories to give some idea of the relationships of the fauna. When the thoroughness with which the present collection was made is considered, it is unlikely that any major components of the isopod fauna have been overlooked, thus zoogeographical conclusions may be made with a fair degree of confidence. The following lists reflect the various categories into which the fauna has been divided, and the percentage of the total number of species they constitute.

Species endemic to St Paul and Amsterdam Islands—10 species—27%

Munnogonium subtilis
Coulmannia unicornis
Cymodocella sapmeri
Dynamenella brunnea
Echinomunna uroventralis
Eisothistos crateris
Ianisera trepidus
Jaeropsis beuroisi
Panathura amstelodami
Paridotea nitida

Species with Antarctic, Subantarctic, and South American Affinities—7 species—18,9%

Antias dimorphus
Antias hispidus
Antias hofsteni
Caecianiropsis ectiformis
Cleantis granulosa
Jaeropsis paulensis
Munna nana

Species with widespread distribution—7 species—18,9%

Aega antillensis
Anatanais gracilis
Idotea metallica
Leptochelia savignyi
Limnoria quadripunctata
Lironeca raynaudii
Porcellio scaber

*Species found only in southern Africa and St Paul and Amsterdam Islands—13 species—*35,1% (*with southern African distribution*)

Aega monilis	Table Bay, East London
Cirolana rugicauda	Port Nolloth, St Helena Bay
Deto echinata	Rocky Point, S.W.A. to Knysna
Dynamenella dioxus	Lüderitzbucht to False Bay
Ianiroides angusta	False Bay
Ianiropsis palpalis	Lüderitzbucht to East London
Janira capensis	Lüderitzbucht to False Bay
Leptochelia barnardi	Table Bay, False Bay
Panathura serricauda	Lüderitzbucht to False Bay
Paridotea reticulata	Lüderitzbucht to False Bay
Parisocladus perforatus	Rocky Point, S.W.A. to East London
Stenetrium crassimanus	False Bay to Natal
Stenetrium saldanha	Saldanha Bay, False Bay, Still Bay

Endemism

The degree of certainty with which the endemism of an area can be described is obviously related to the degree to which surrounding areas have been sampled. As four of the endemics in the present list range in depth from 30 to 120 metres—a depth range not often well sampled, these cannot be regarded as endemics with any certainty. Nevertheless, the figure of 27 per cent agrees well with that for the fish of St Paul and Amsterdam Islands given by Briggs (1974) of 28 per cent.

Southern African/St Paul and Amsterdam species

Twelve of the thirteen species in this category are typical of the cold west coast of South Africa, several being known only from Lüderitzbucht to False Bay. Three species extend to East London or Durban on the east coast; of these, *Aega monilis* is a fish parasite, while the other two are asellote isopods with a predominantly subtidal distribution, and may be considered as within Stephenson's (1947) southern warm–temperate province stretching (*in senso stricto*) from Cape Agulhas to Algoa Bay.

Knox (1960) regards St Paul and Amsterdam as a separate cold-temperate province of the austral sea, not especially related to southern Africa. Briggs (1974: 151), however, considering seven of the ten non-endemic species of fish of these islands which also occur in southern Africa, regards St Paul and Amsterdam as more probably related to the 'Cape of Good Hope . . . within the southern Africa Warm-Temperate Region'. Stephenson, with a detailed knowledge of the intertidal of southern Africa, regarded the west coast of South Africa from about Cape Point to Tropical West Africa as a cold-temperate province. As twelve of the thirteen isopod species common to South Africa and St Paul–Amsterdam may be regarded as typical cold-temperate west coast inhabitants, Briggs's view of a warm-temperate fauna is misleading, as is Knox's view of an unrelated cold-temperate fauna.

A more accurate view, supported by the isopods and the fish, is that the St Paul and Amsterdam Islands have a cold-temperate fauna, with a marked affinity to the cold-temperate west coast fauna of South Africa, but that a small warm-temperate component related to the warm-temperate south coast fauna of South Africa is also present. An example of this latter component is *Stenetrium crassimanus*, known from False Bay to Natal. Comparison of the sea-surface temperatures of the two areas gives further weight to this view. St Paul and Amsterdam have an average summer temperature of 17,5°C, and average winter temperature of 12,5°C (Wyrtki 1971; Briggs 1974), while on the west coast of South Africa the annual inshore temperature ranges from 10°–16°C (Division of Sea Fisheries Report *33*).

The presence of a large number of South African species amongst the isopod fauna of St Paul and Amsterdam as well as other organisms common to both areas, such as the portunid crab *Ovalipes trimaculatus* (Arnaud, Beurois & Noel 1972) and various algae including *Splachnidium rugosum* and the kelp *Macrocystis pyrifera* (Briggs 1974), may easily be explained by invoking the effect of the West Wind Drift, as noted by Briggs (1974: 150).

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Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

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Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (figs 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

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Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

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BRIAN KENSLEY

ISOPODAN AND TANAIDACEAN CRUSTACEA FROM THE ST PAUL AND AMSTERDAM ISLANDS, SOUTHERN INDIAN OCEAN

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FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines.—*Archs Zool. exp. gén.* **74**: 627–634.
KOHN, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon.—*Ann. Mag. nat. Hist.* (13) **2**: 309–320.
KOHN, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean.—*Bull. Bingham oceanogr. Coll.* **17** (4): 1–51.
THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* **4**: 269–270. Jena: Fischer.—*Denkschr. med.-naturw. Ges. Jena* **16**: 269–270.

(*continued inside back cover*)

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PLIOCENE GIRAFFOIDEA (MAMMALIA, ARTIODACTYLA) FROM THE CAPE PROVINCE

By

JOHN M. HARRIS

Cape Town Kaapstad

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(With 9 figures and 10 tables)

[*MS. accepted 8 April 1976*]

CONTENTS

	PAGE
Introduction	325
Systematics	326
Sivatherium hendeyi sp. nov.	328
Giraffa cf. *G. jumae*	347
Discussion	352
Acknowledgements	352
References	353
Abbreviations	353

ABSTRACT

One sivathere species and one giraffine species, both represented by ossicones, teeth and postcranial elements, have been recovered from 'E' Quarry at Langebaanweg. The sivathere remains appear more primitive than those of the common African sivathere, *S. maurusium*, and warrant the creation of a new species. The giraffine species is less abundantly represented and is very similar to *Giraffa jumae* from east African Pliocene and Pleistocene localities. Other faunal evidence from 'E' Quarry suggests an early Pliocene age for the Varswater Formation. The *Sivatherium* species supports such an interpretation, suggesting that the Langebaanweg giraffoids are the earliest representatives yet reported of their respective genera.

INTRODUCTION

In recent years a number of Pliocene mammalian assemblages have been recorded from east and north Africa, but from South Africa only the local faunas from 'E' Quarry, Langebaanweg, are of undoubted Pliocene age. The younger material from Baard's Quarry at Langebaanweg is not considered in this paper. Hence all subsequent references to 'Langebaanweg' refer solely to 'E' Quarry.

Two local faunas are recognized in the Varswater Formation at Langebaanweg but the earlier, from the Quartzose Sand Member, is of similar faunal composition to the later local fauna from the superjacent Pelletal Phosphorite Member. Summaries of the local faunas and geology of the Langebaanweg locality have been published (Hendey 1974, 1976*a*; Tankard 1975) as have detailed descriptions of some of the faunal elements (Maglio & Hendey 1970; Hendey 1972; Hendey & Repenning 1972; Hooijer 1972). The fossiliferous sediments cannot be dated by radiometric methods and, though the fossiliferous

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horizons are associated with a marine transgression, chronological evidence from marine invertebrate faunas has so far proved inconclusive (Hendey, pers. comm.).

The Langebaanweg local faunas include a number of exotic taxa unrepresented elsewhere in Africa (Hendey 1972; Hendey & Repenning 1972; Hendey 1976*b*), but other elements of the fauna may, when studied in detail, afford the best means of gauging the age of the Langebaanweg deposits relative to other fossil mammal localities. The Langebaanweg rhinoceros (Hooijer 1972) suggests chronological equivalence with east African sites dated at or more than 4 m.y. Elephantid remains from 'E' Quarry suggest equivalence with Mursi and Kanapoi (Maglio 1973: 73; Maglio & Hendey 1970). Available evidence from the Langebaanweg Suinae suggests an age of between 4 and 5 m.y. (Harris & White, in preparation). The Langebaanweg giraffoids tend to support these interpretations and the *Sivatherium* appears more primitive than other African occurrences of this genus. It will be interesting to see in due course the relative ages suggested by other mammalian groups.

All specimens referred to in the text or tables with the prefix L are from 'E' Quarry, Langebaanweg. The full prefix for such specimens is SAM–PQ–L.

All measurements given in Tables 1–10 are in millimetres.

SYSTEMATICS

Superfamily GIRAFFOIDEA Simpson, 1931

Following his study of the Miocene giraffoids from east and north Africa, Hamilton (1973) extracted the sivatheres from the family Giraffidae and placed them into a new family Sivatheriidae. His interpretation that the family Giraffidae included only two subfamilies—the Paleotraginae and Giraffinae—is followed here. Two giraffoid species are recognized from Langebaanweg—a sivatheriid represented by nearly 200 specimens and a giraffine represented by over 80 specimens.

Family **Sivatheriidae** Hamilton, 1973

Six sivatheriid genera are recognized from Eurasia and Africa and may be readily distinguished by their ossicone morphology. The frontal bones of *Prolibytherium*, a genus restricted to the early Miocene of north Africa, support large aliform ossicones that have anterior and posterior palmations (Hamilton 1973). *Helladotherium*, known from the early Pliocene of Eurasia (and questionably recorded from north Africa), apparently lacks ossicones and may indeed be a female of *Hydaspitherium* or *Bramatherium* (Matthew 1929; Colbert 1935). *Hydaspitherium*, from the middle Pliocene of Asia, is a gigantic sivatheriid with two ossicones fused at their base into one solid mass on the frontoparietal region (Colbert 1935). *Birgerbohlinea*, from the early Pliocene of Spain, possesses two rounded vertical ossicones that are also strongly connected at their base (Crusafont 1952). *Bramatherium* from the middle Pliocene of Asia has four ossicones

—a large pair growing upward from the frontoparietal region and a smaller pair extending laterally from the parietals (Colbert 1935). Male specimens of *Sivatherium giganteum* from the late Pliocene and Pleistocene of Asia also possess two pairs of ossicones—a small pair arising from the frontal region and a larger pair extending nearly vertically from the parietal region. It is clear from both ossicone and dental morphology that the Pliocene and Pleistocene sivatheriids from Africa are more closely related to *Sivatherium* than to other Eurasian genera and their consequent allocation to this genus seems justified.

Sivatherium Falconer & Cautley, 1835

A diagnosis of this genus is given in Harris (1976). Previously recorded specimens of African sivatheriids exhibit a number of differences from the Asian genotype *Sivatherium giganteum*. Only one relatively complete cranium is known from Africa. This specimen, from the Pleistocene of northern Kenya (Harris 1976), differs from *S. giganteum* in having a longer facial region and a narrower and less deep cranial region. The posterior ossicones of recorded African sivatheriids are orientated differently from the Asian species and the anterior ossicones, if interpreted as such, are sited more posteriorly and are less prominently developed (Harris 1974). The teeth of Asian and African *Sivatherium* specimens are, however, similar in morphology. Nevertheless the cranial differences, and particularly those of the ossicones, are sufficient to warrant taxonomic separation from *S. giganteum*.

Owing to the fragmentary nature of much of the material, a number of difficulties are encountered in attempting to identify African sivatheriids to species level. In their monograph on the fossil giraffoids of Africa, Singer & Boné (1960) recognized six different taxa:

Libytherium maurusium
Sivatherium olduvaiense
S. olduvaiense haughtoni
S. olduvaiense vanhoepeni
S. olduvaiense subsp. indet.
Sivatherium cingulatum

As subsequently noted (Churcher 1974; Harris 1974), the type mandible of *L. maurusium* was found by Arambourg (1960) to have been wrongly restored. Arambourg's new restoration clearly showed that *L. maurusium* and *S. olduvaiense* were conspecific and that the common African sivathere should be called *Sivatherium maurusium*.

With regard to the other taxa recognized by Singer & Boné (1960) it is evident that the type (and only) upper molar of *S. cingulatum*, the type (and only) lower molar fragment of *S. olduvaiense haughtoni*, the four incomplete teeth from Tierfontein assigned to *S. olduvaiense* subsp. indet. and an incomplete lower molar from Florisbad assigned to *S. olduvaiense* are all larger than the range of variation exhibited by other specimens assigned to *S. maurusium*.

Tierfontein, Florisbad and Cornelia are all middle to late Pleistocene sites and the provenance of the other large specimens is poorly substantiated other than that they come from the 'Vaal River Gravels'. It is entirely possible that these large teeth from the Orange Free State and the Cape Province are from late South African representatives of *S. maurusium*, especially as the ossicones from Tierfontein may unequivocally be assigned to this species. If so, then nearly all the African sivatheriids reported to date can be assigned, or at least referred, to a single species.

South African material that is more directly comparable to east and north African specimens of *S. maurusium* has been collected from Elandsfontein (Singer & Boné 1960). The Elandsfontein material includes deciduous and permanent teeth, posterior ossicones and metapodials. A few deciduous and permanent teeth are known from Makapansgat but, in the absence of ossicones from that site, cannot be identified to species. A single unerupted *Sivatherium* molar is also known from Swartkrans (Churcher 1974).

There is currently no evidence to support more than one species of *Sivatherium* from Langebaanweg. If an early Pliocene age is corroborated by subsequent investigation of other fossil mammals from that locality the Langebaanweg *Sivatherium* would appear to be the earliest record of the genus. The sivathere from this locality possesses conical anterior ossicones that are present also in the Asian species but absent in *S. maurusium*. The posterior ossicones of the Langebaanweg form are not, however, palmate and near-vertically orientated as in *S. giganteum*, but extend backwards and outwards from the cranium as in the common morph of *S. maurusium* (Type A of Harris 1974). Several posterior ossicones are known from Langebaanweg and all may be distinguished from those of *S. maurusium* by their lack of ornamentation in terms of knobs and flanges.

African *Sivatherium* ossicones are quite variable in morphology although all apparently conform to one of three basic shapes (Harris 1974). The ossicones are present only in male specimens and the degree of ornamentation may well be a function of the age of the individual (cf. secondary bone apposition in extant male giraffes). It is possible therefore that the Langebaanweg sivathere ossicones, like those of the Langebaanweg giraffines, are all from immature individuals. On balance, however, the erection of a new species for the Langebaanweg sivathere appears warranted on morphological grounds.

Sivatherium hendeyi sp. nov.

Figs 1–7

Sivatherium olduvaiense (Hopwood): Singer & Boné, 1960: 544–5.
Libytherium olduvaiense (Hopwood): Hendey, 1970: 98.

Holotype

SAM–PQ–L12730, virtually complete left ossicone from the Quartzose Sand Member of the Varswater Formation in 'E' Quarry, Langebaanweg.

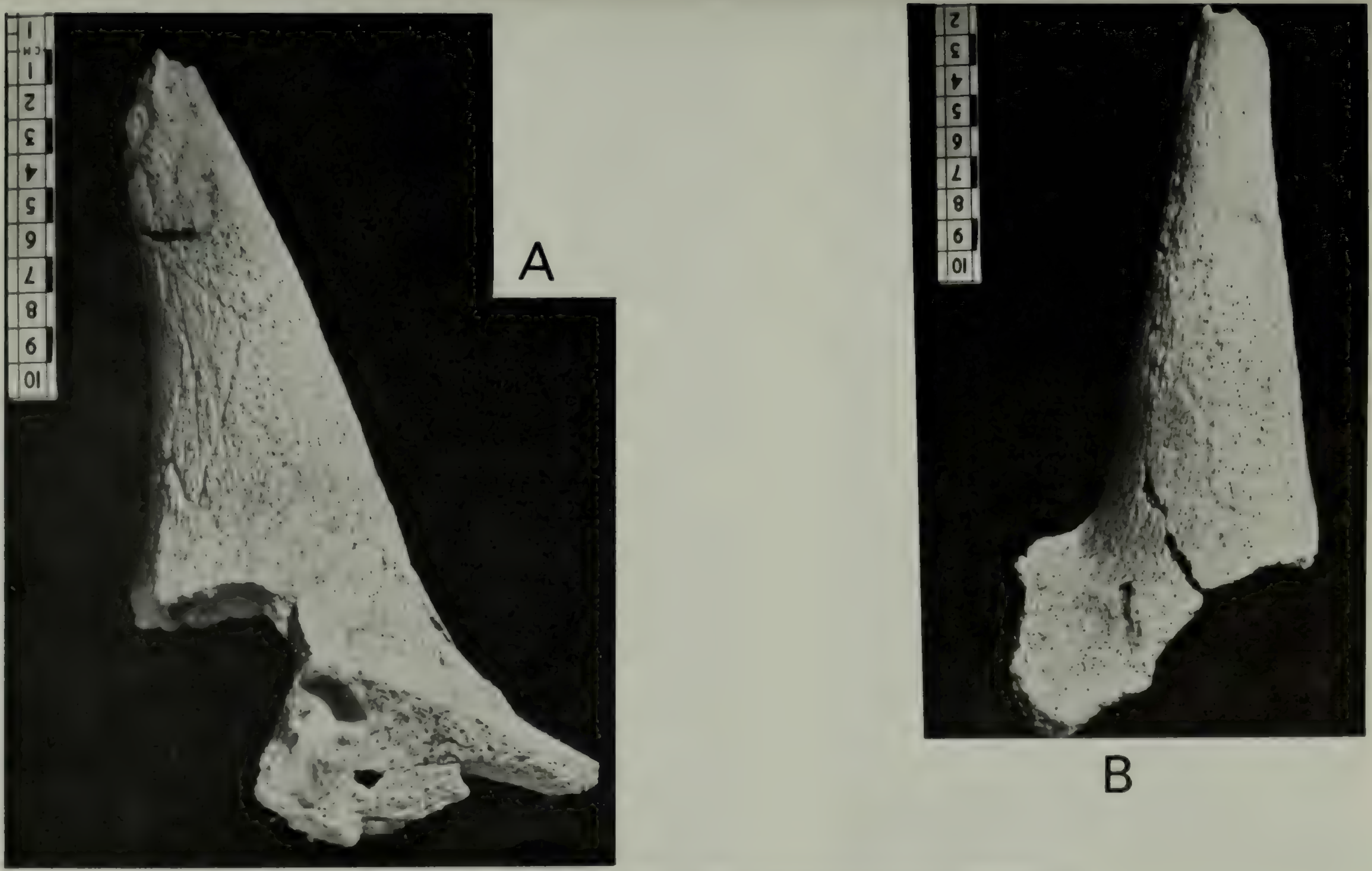

Fig. 1. *Sivatherium hendeyi* left anterior ossiocone (SAM–PQ–L31285, paratype).
A. Medial view. B. Anterior view.

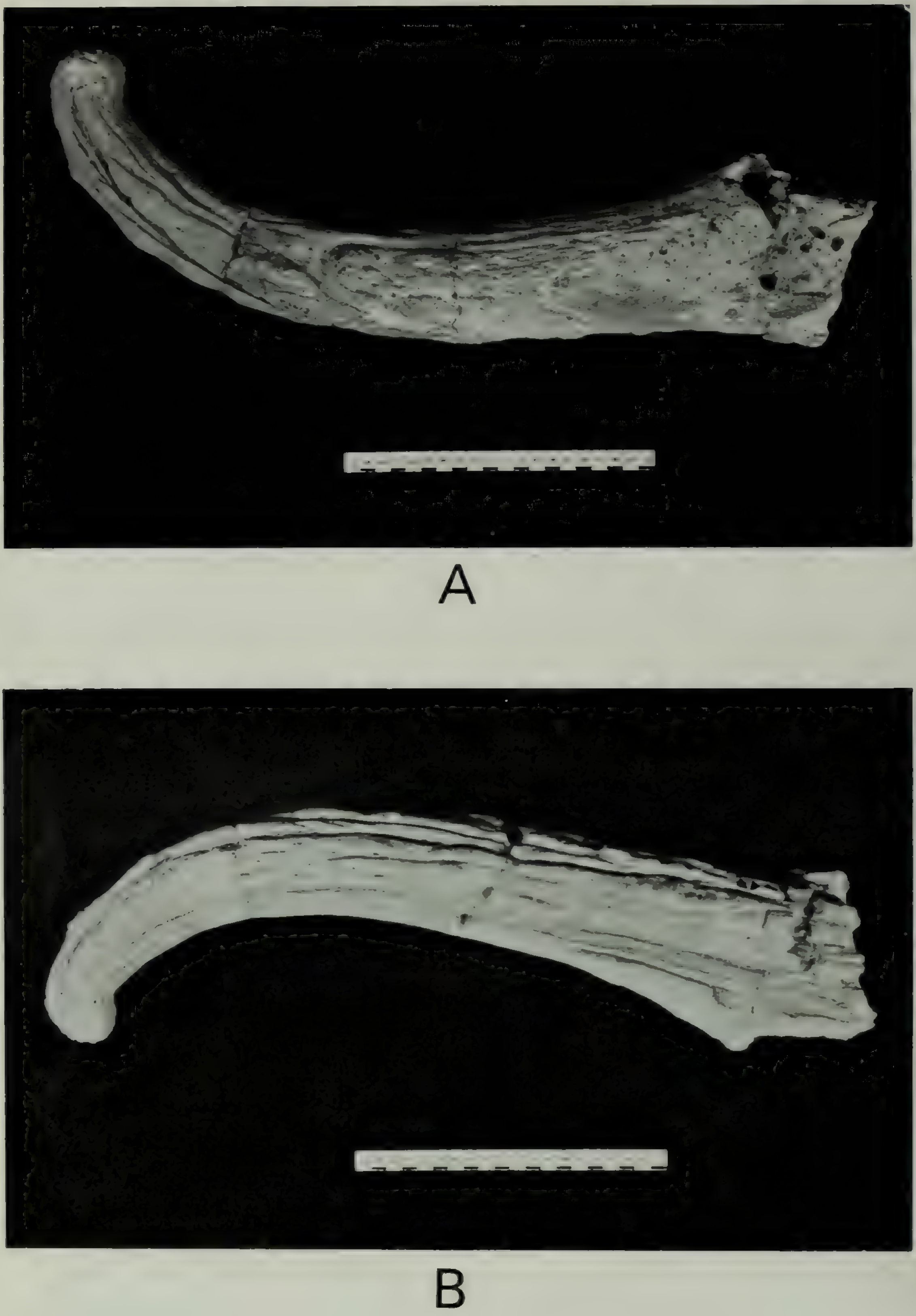

Fig. 2. *Sivatherium hendeyi* left posterior ossicone (SAM–PQ–L12730, holotype). A. Ventral view. B. Dorsal view.

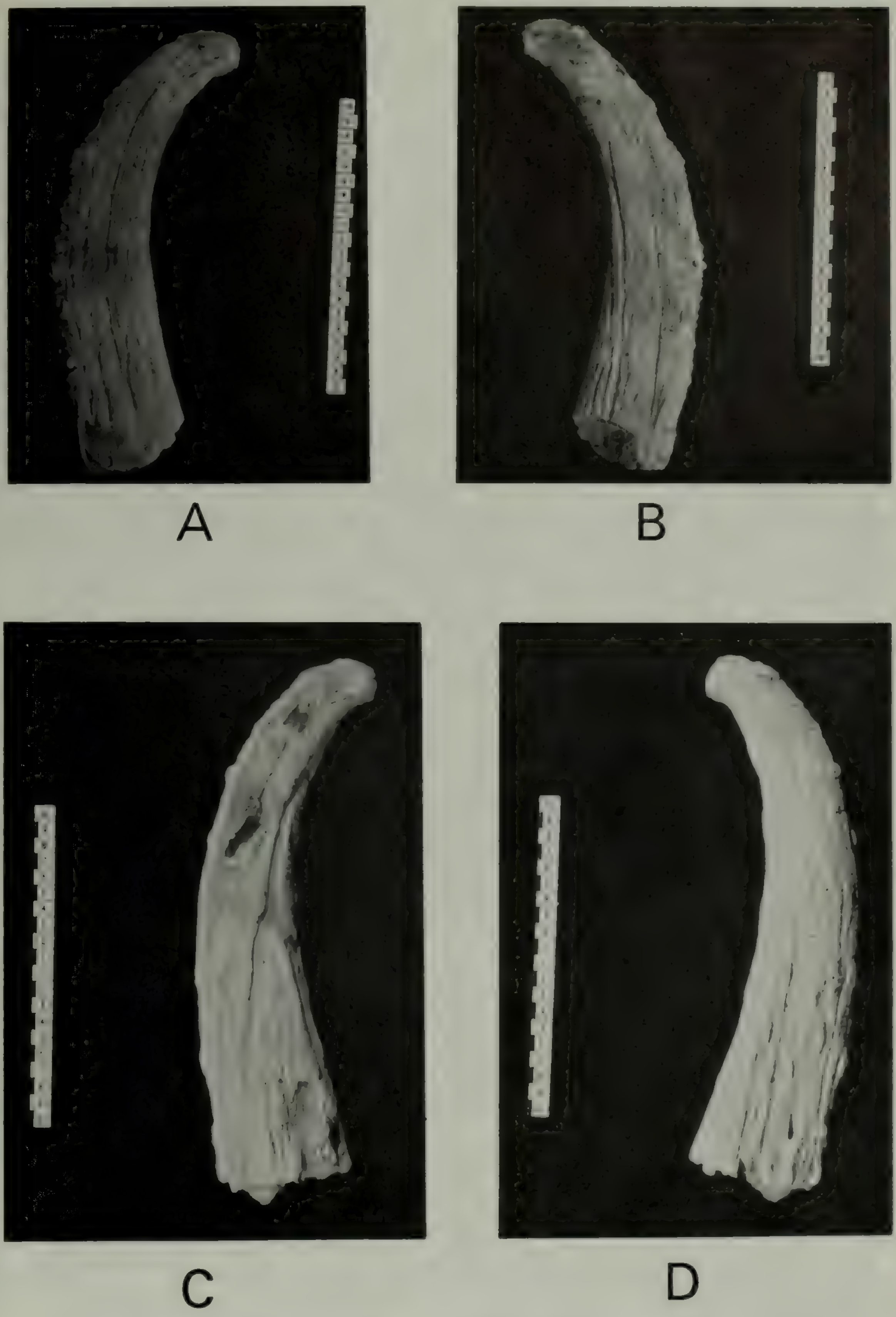

Fig. 3. *Sivatherium hendeyi* incomplete posterior ossiocones.

A. SAM–PQ–L7243, right posterior ossicone, dorsal view.
B. SAM–PQ–L7243, right posterior ossicone, ventral view.
C. SAM–PQ–L7244, left posterior ossicone, ventral view.
D. SAM–PQ–L7244, left posterior ossicone, dorsal view.

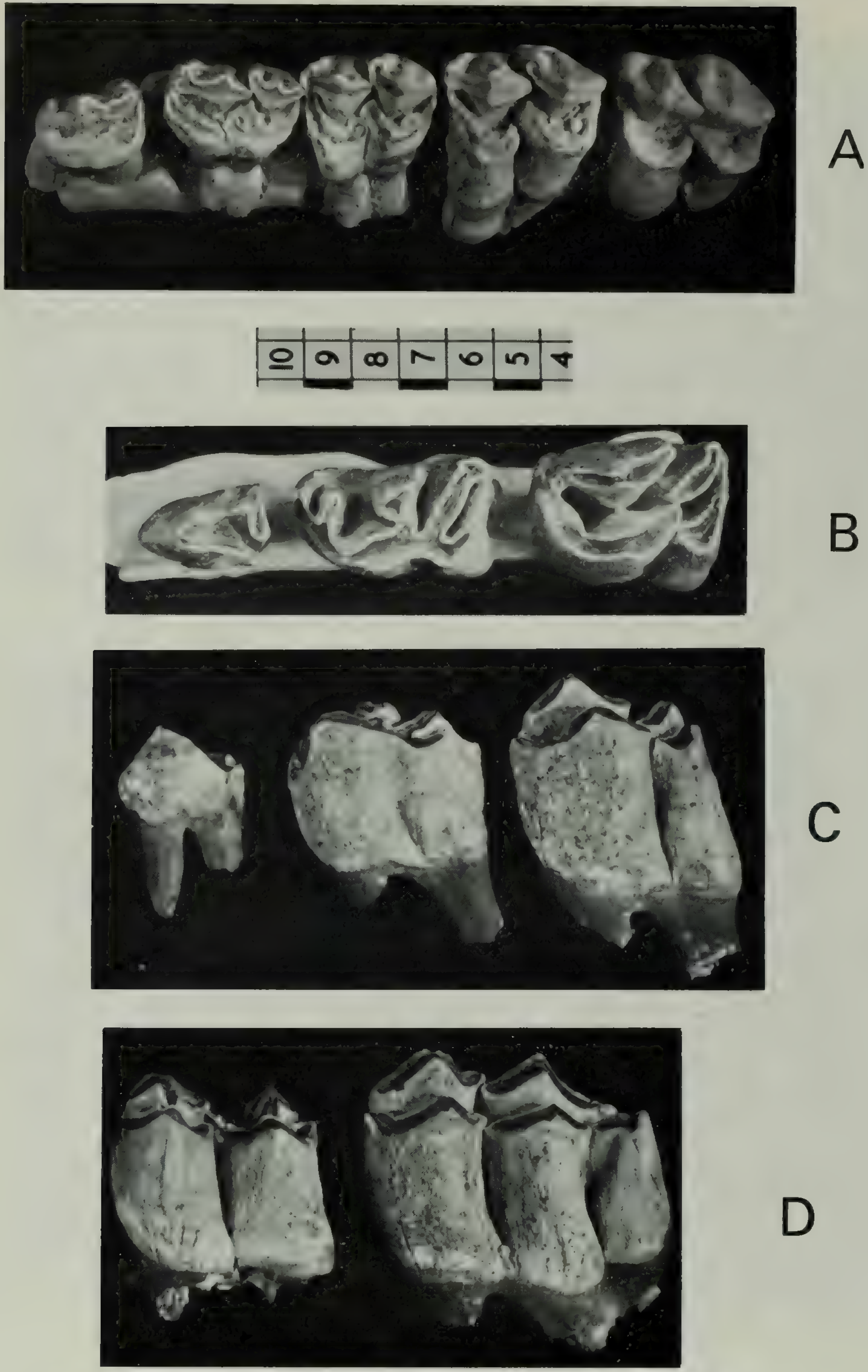

Fig. 4. Giraffoid dentitions from 'E' Quarry, Langebaanweg.

A. SAM–PQ–L10343, *Giraffa* cf. *G. jumae* upper dentition (LDP^2–M^2), occlusal view. B. SAM–PQ–L31137, *Sivatherium hendeyi* lower dentition (LP_{2-4}), occlusal view. C. SAM–PQ–L31137, *Sivatherium hendeyi* lower dentition (LP_{2-4}), lateral view. D. SAM–PQ–L31137, *Sivatherium hendeyi* lower dentition (LM_1, LM_3), lateral view.

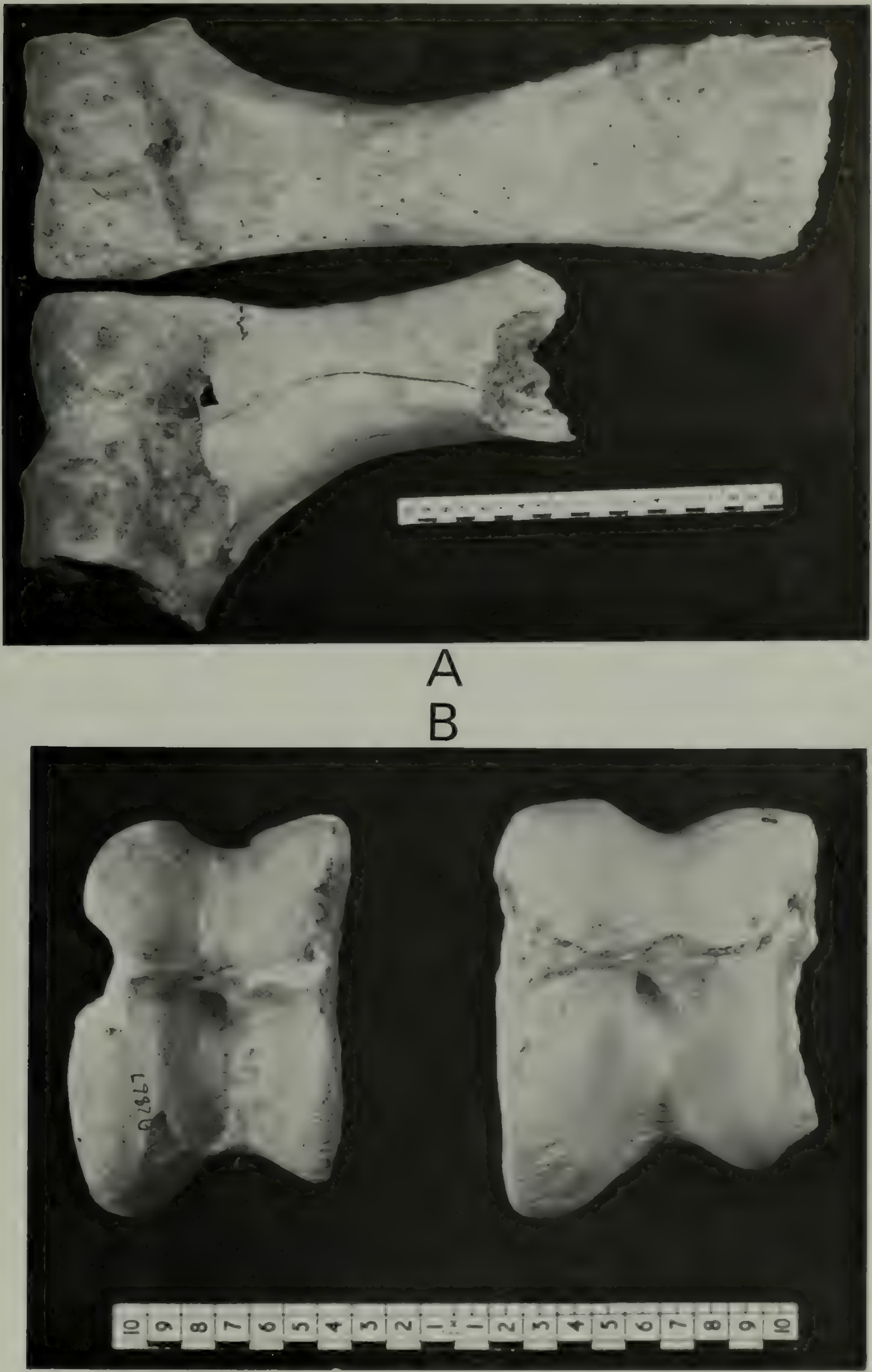

Fig. 5. Giraffoid postcranial elements from Langebaanweg.

A. Distal humeri of *Giraffa* cf. *G. jumae* (top) and *Sivatherium hendeyi* (bottom), anterior view.
B. Left astragali of *Giraffa* cf. *G. jumae* (left) and *Sivatherium hendeyi* (right), anterior view.

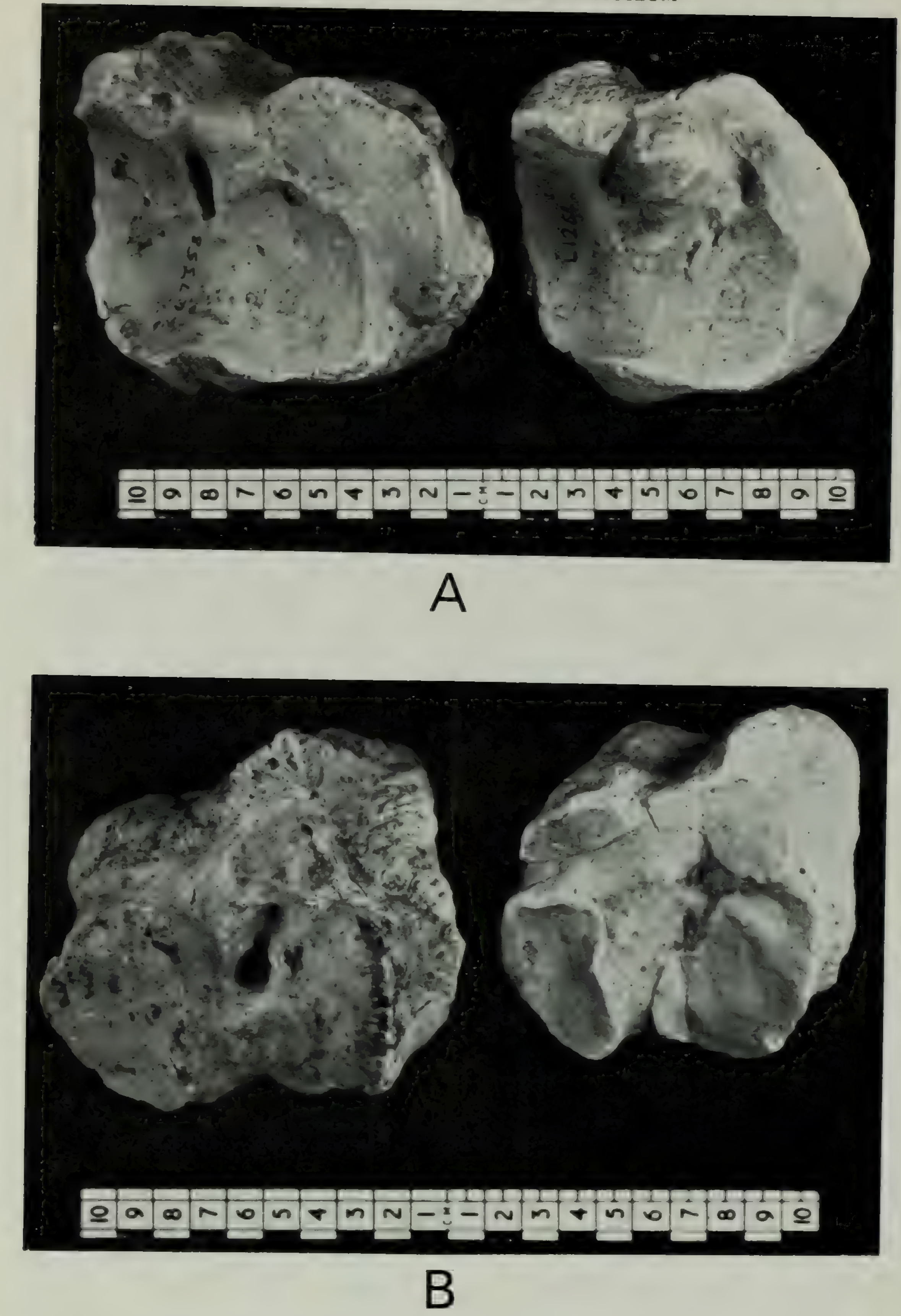

Fig. 6. Giraffoid naviculocuboids from Langebaanweg.
A. Left naviculocuboids of *Sivatherium hendeyi* (left) and *Giraffa* cf. *G jumae* (right), proximal view. B. left naviculocuboids of *Sivatherium hendeyi* (left) and *Giraffa* cf. *G. jumae* (right), distal view.

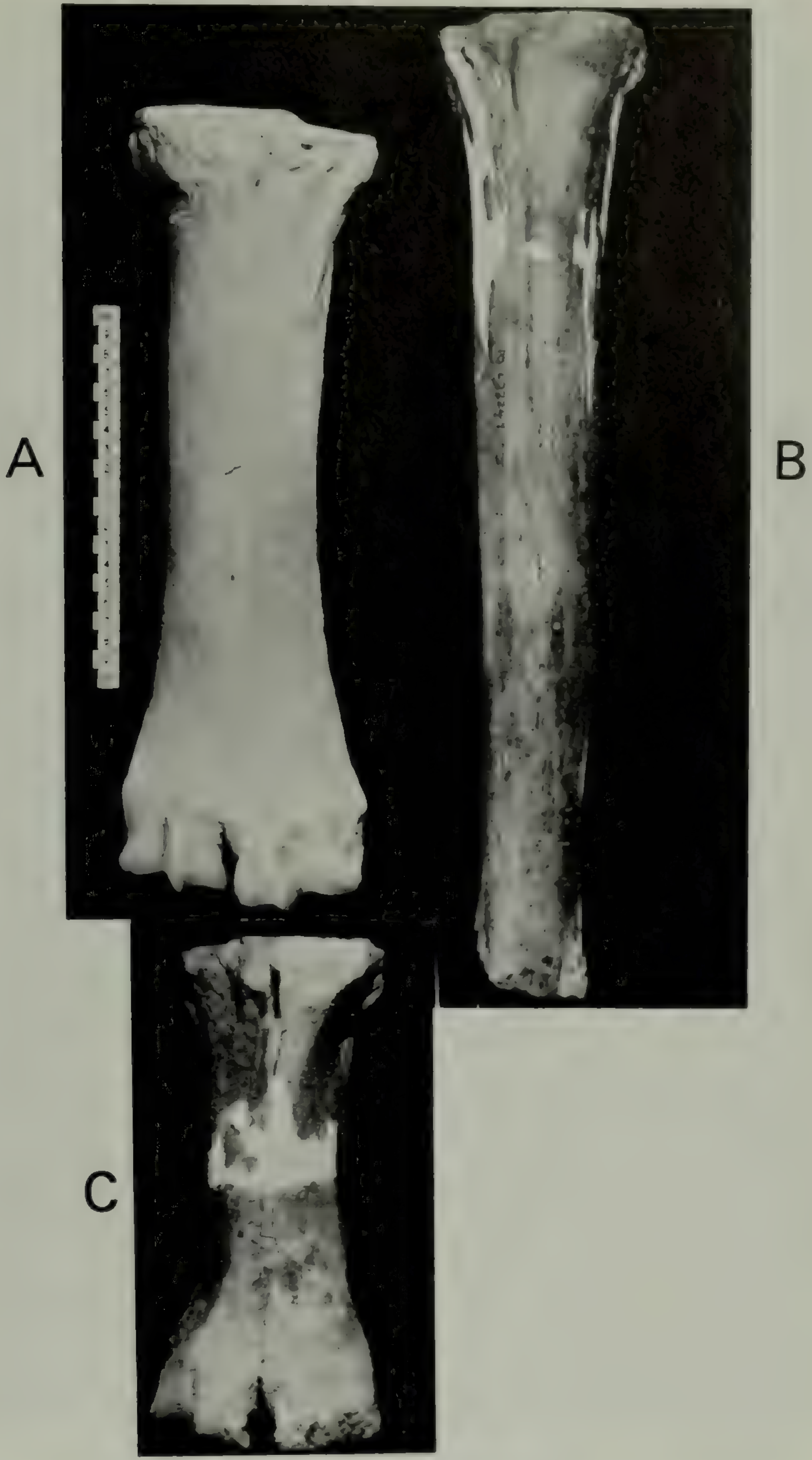

Fig. 7. Giraffoid metacarpals.

A. Left metacarpal of *Sivatherium hendeyi* from Langebaanweg, anterior view. B. Proximal right metacarpal of *Giraffa* cf. *G. jumae* from Langebaanweg, anterior view. C. Right metacarpal of *Sivatherium maurusium* from Elandsfontein, anterior view.

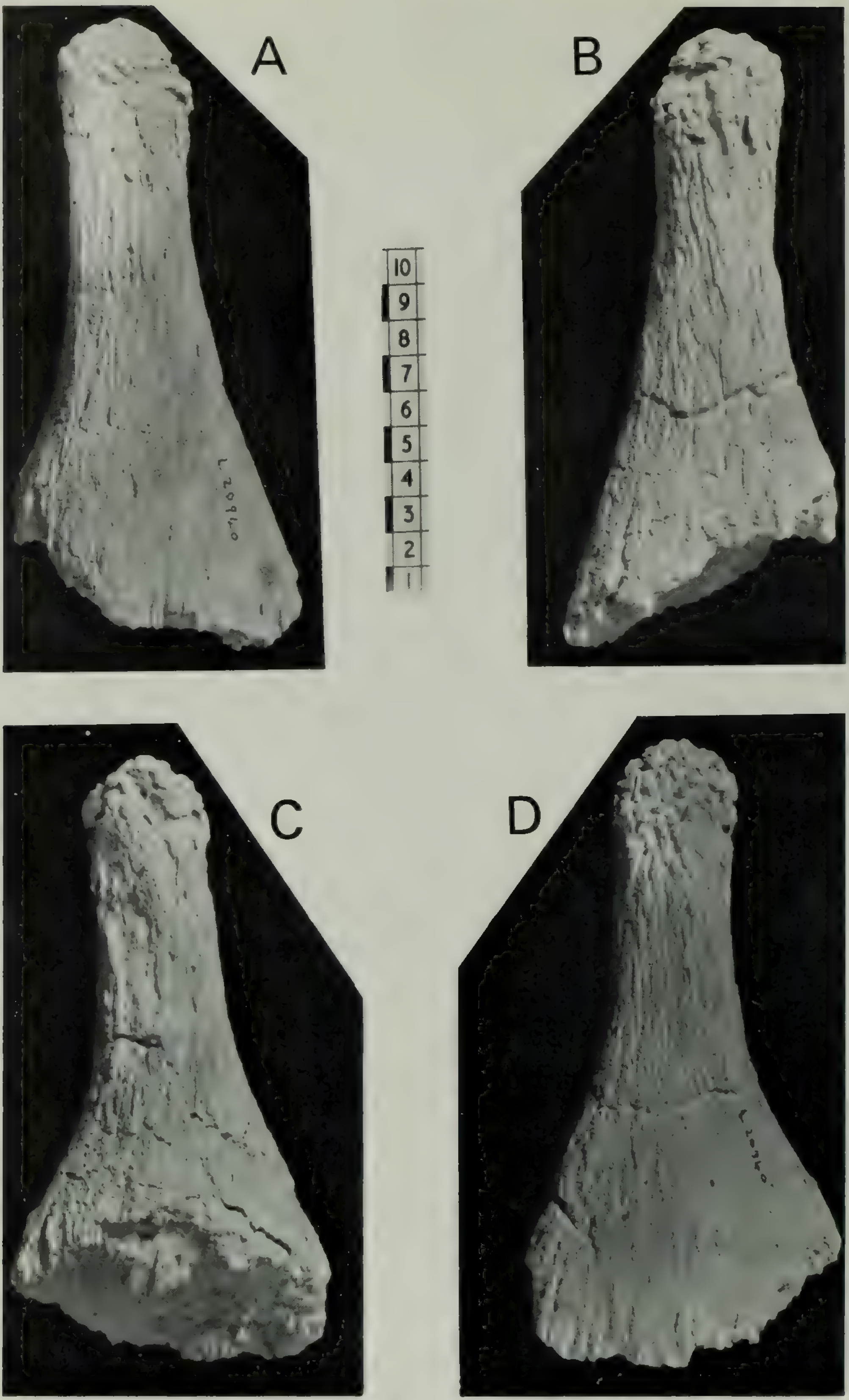

Fig. 8. Ossicones of *Giraffa* cf. *G. jumae* from Langebaanweg.

A. SAM–PQ–L20490, *Giraffa* cf. *G. jumae* left ossicone, medial view. B. SAM–PQ–L20940, *Giraffa* cf. *G. jumae* left ossiocone, lateral view. C. SAM–PQ–L20940, *Giraffa* cf. *G. jumae* right ossicone, lateral view. D. SAM–PQ–L20490, *Giraffa* cf. *G. jumae* right ossicone, medial view.

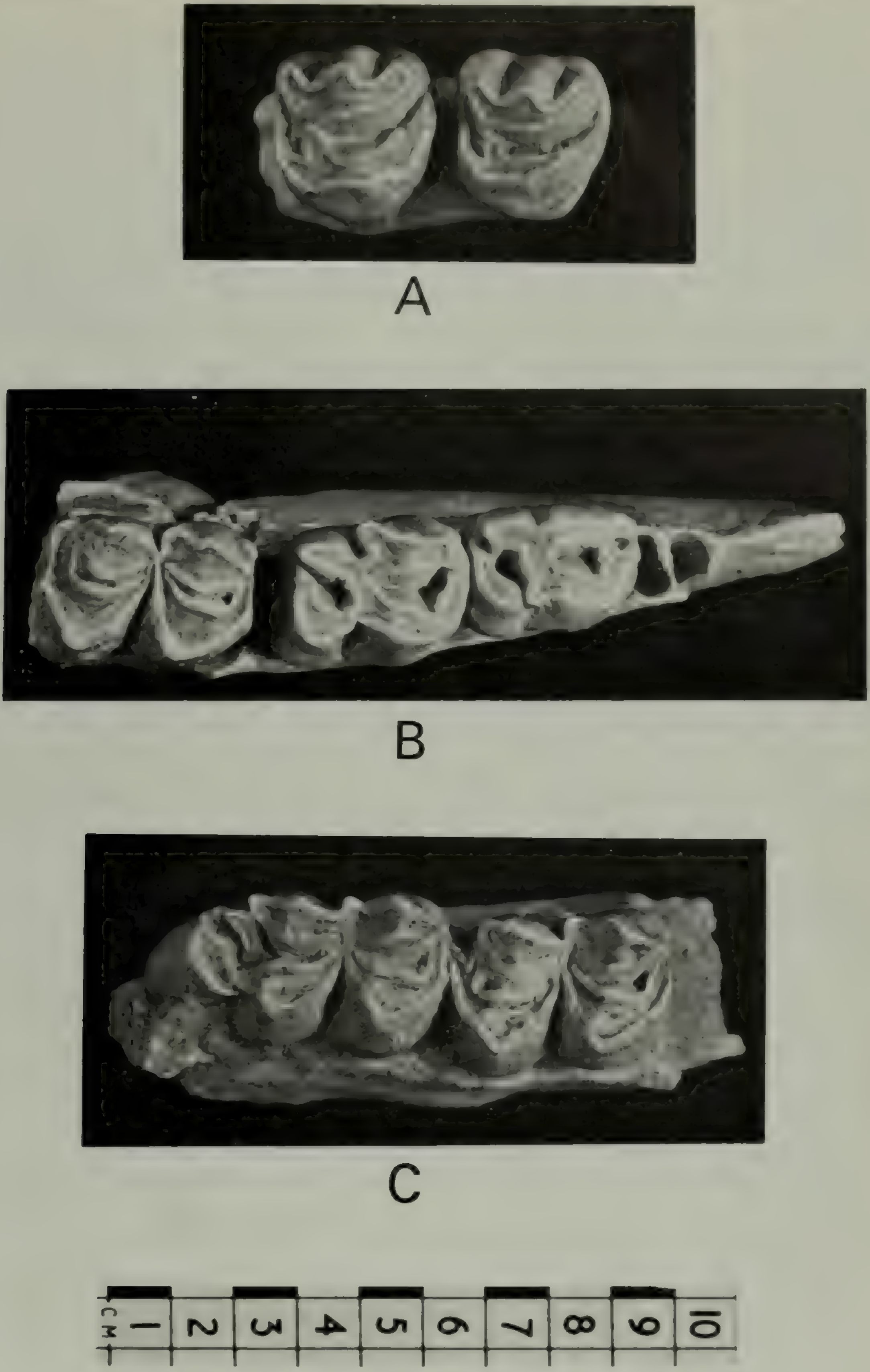

Fig. 9. Teeth of *Giraffa* cf. *G. jumae* from Langebaanweg.

A. SAM–PQ–L30126, *Giraffa* cf. *G. jumae* upper premolars (RP$^{3-4}$), occlusal view. B. SAM–PQ–L31138, *Giraffa* cf. *G. jumae* partial right mandible (RP$_3$–M$_1$), occlusal view. C. SAM–PQ–L31138, *Giraffa* cf. *G. jumae* partial right mandible (M$_{2-3}$), occlusal view.

Paratype

SAM–PQ–L31285, right and left anterior ossicones from the Pelletal Phosphorite Member of the Varswater Formation in 'E' Quarry, Langebaanweg.

Diagnosis

Species of *Sivatherium* of similar size and dental morphology to *S. giganteum* and *S. maurusium*. Posterior ossicones short, extending laterally and backwards from the cranium and unornamented by knobs and flanges or palmate digitations. Anterior ossicones conical as in *S. giganteum*. Metacarpals longer than in other species of *Sivatherium*.

Etymology

The species is named after Q. B. Hendey, who has been responsible for collecting most of the 'E' Quarry Langebaanweg fauna.

Cranial material

Anterior ossicones

A single pair of anterior ossicones (L31285) has been recovered from the Pelletal Phosphorite Member at Langebaanweg. The left anterior ossicone lacks its distal tip but the base of the ossicone is complete and, on the medial side, extends as far as the intrafrontal suture. The right ossicone is broken distally and the lateral portion of the base is also missing.

The anterior ossicones are conical structures, as in *S. giganteum*, and are slightly compressed mediolaterally (the lateral side being the flatter). They are inclined backwards at an angle of 50° to the cranial vault at the intrafrontal suture. They also diverge outwards from each other. A large basal sinus is present and the adjoining frontal bone is cancellous. The anterior and lateral surfaces of the anterior ossicones are relatively smooth but a number of irregular longitudinal ridges and furrows are present on the posterior surface though less prominent than the grooves on the posterior ossicones.

The anterior ossicones from Langebaanweg would appear to be the first unequivocal specimens from an African sivathere. Anterior ossicones have previously been reported from Tierfontein and Elandsfontein (Singer & Boné 1960, pls 29, 42) but the Tierfontein specimen is almost certainly part of a posterior ossicone while the Elandsfontein specimen is unfortunately no longer available for examination. The similarity of the conical anterior ossicones to those of *Sivatherium giganteum* confirm the relationship of the Pliocene African sivatheres with *Sivatherium* from Asia. Anterior ossicones are not present in the relatively complete sivathere skull from Koobi Fora, Kenya (Harris 1976), and the apparent absence of anterior ossicones from other later Pliocene and Pleistocene accumulations suggests that they are greatly reduced or lost in *S. maurusium*.

Posterior ossicones

No complete posterior ossicone is known from Langebaanweg although L12730 is virtually complete and apparently lacks only a few centimetres of bone from its junction with the cranial vault. Other less complete specimens include L2542 (right ossicone fragment), L3690 (dorsal fragment of proximal right ossicone), L4083 (ventral fragment proximal right ossicone), L7243 (distal right ossicone), L7244 (distal left ossicone), L7245 (posterior fragment of proximal right ossicone), L7246 (fragment of proximal ossicone) and L6247 (fragment of proximal left ossicone).

The posterior ossicone morphology is closest to Type A of Harris (1974), extending outwards and backwards from the cranial vault and perhaps slightly upwards at the distal tip. The ossicones exhibit only a faint degree of torsion (anticlockwise in the right ossicone). Near the base each ossicone is almost triangular in transverse section with a flat dorsal surface and a strongly convex ventral surface. The distal third is more rounded and is almost circular in transverse section. The posterior and ventral surfaces are smooth for almost their entire length. The anterior and dorsal surfaces are sculpted by deep and wide longitudinal grooves that through torsion extend on to the ventral surface in the distal portion of the ossicone. The intervening ridges are rugose on the anterior surface of the proximal portion of the ossicones and again at intervals on the distal portion. These rugosities are interpreted to foreshadow the flange and discrete knobs that are a distinctive feature of specimens of *S. maurusium*. The longitudinal grooves of the dorsal surface of the ossicone are less deep and less numerous than those of the anterior surface. Each ossicone terminates in a distinct bulbous knob.

The low degree of torsion, small size, small basal sinus, virtual absence of grooves on the ventral surface and lack of flanges and knobs on the posterior ossicones when taken in conjunction with the discrete conical anterior ossicones serve to distinguish *S. hendeyi* from *S. maurusium*. It is likely, none the less, that the latter evolved from the former.

Dentition

Although a couple of reasonably complete lower dentitions are known, most of the Langebaanweg sivathere teeth comprise isolated specimens. The more complete specimens are listed in the tables of dental measurements (Tables 2–4). The teeth of *S. hendeyi* are morphologically indistinguishable from those of *S. maurusium* and are of similar size to the *S. maurusium* teeth from the near-by but later locality of Elandsfontein. The Elandsfontein and Langebaanweg sivathere teeth are larger than those from Makapansgat but smaller than comparable specimens from the Vaal River localities.

Postcranial material

A large number of giraffoid postcranial elements have been recovered from the Varswater Formation. The apparent presence of only one giraffine and one sivatheriid species and the occurrence of associated skeletal elements permit ready identification of *Sivatherium* versus *Giraffa* postcranial elements. Accession numbers of *Sivatherium* limb bones are given in the tables of measurements. Observed differences between the Langebaanweg sivatheriid and giraffine skeletal elements are listed below.

Scapula

It is difficult if not impossible to separate scapulae of *Sivatherium* from those of *Giraffa* solely on fragments of the glenoid. Specimens larger than those of extant *G. camelopardalis* almost certainly belong to *Sivatherium* but smaller specimens may represent either *Giraffa* or immature *Sivatherium* individuals. The posterior border of the blade is distinctly more rounded in *Sivatherium*, but this feature can be used only for the more complete specimens which, by virtue of the relative fragility of the blade, are rare in the fossil record.

Humerus

No complete or proximal giraffoid humeri are known from Langebaanweg but several distal epiphyses, some with distal portions of the shaft, have been collected. *Sivatherium* humeri tend to be larger in overall size and with shorter but relatively more massive diaphyses than those of giraffines. The distal portion of the shaft widens to meet the lateral epicondyle more rapidly than in *Giraffa*. The coronoid fossa is smaller and less deep in *Sivatherium*. The posterior articular surface of the lateral condyle is smaller in *Sivatherium* and the area for attachment of the extensor digitalis communis is larger.

Ulna

The semilunar notch of the *Sivatherium* ulna is proportionately larger and wider than in Giraffa. It is divided into two unequal halves by a low ridge but, unlike in *Giraffa*, the lateral portion is larger than the medial. The semilunar notch extends for the entire width of the ulna in *Sivatherium* but not in *Giraffa*. Distal to the semilunar notch the lateral facet for articulation with the radius is much shorter in *Giraffa*.

Radius

The radius of *Sivatherium* is proportionately shorter and less straight than that of *Giraffa* although more massive. The notch dividing the medial from the lateral facet in the proximal epiphysis extends for nearly half the craniocaudal length of the epiphysis in *Sivatherium* but is much shorter in *Giraffa*. The distal epiphysis is of similar morphology to that of *Giraffa* but is wider laterally. On the caudal edge of the distal epiphysis the articular facets extend farther proximally but the styloid process of the ulna extends less far posteriorly in *Sivatherium* than in *Giraffa*.

Metacarpals

Sivatherium metacarpals closely resemble those of *Giraffa* but are shorter, wider and with larger epiphyses. Most specimens from Langebaanweg comprise either proximal or distal epiphyses. The distal epiphysis of the sivathere metacarpal may be distinguished from that of *Giraffa* by its larger size and proportionately wider epiphyseal region. Proximal epiphyses may be separated by the same factors but, in addition, the lateral facet of the proximal epiphysis is normally less widely separated from the medial facet at its posterior edge in *Giraffa*. The shaft of the sivathere metacarpal is proportionately less deep craniocaudally.

Tibia

Sivatherium tibiae are shorter but proportionately more massive than those of giraffine species. The proximal epiphysis is of similar width to that of *Giraffa* but is relatively longer craniocaudally. The cnemal crest, extending distally from the proximal epiphysis, is stout and extends nearly half-way down the shaft. In *Giraffa* the cnemal crest is less prominent and is confined to the proximal third of the shaft. Moreover the central and distal portions of the shaft are more craniocaudally compressed in *Giraffa*. In the distal epiphysis the articular facets for the fibula are more horizontally aligned in *Sivatherium*, those of giraffine tibiae being inclined more steeply towards the lateral edge of the epiphysis.

Fibula

Sivatherium fibulae are rather smaller in overall size than those of *Giraffa* and the tibial facets are less wide, less elongate and have greater relief. The anterior tibial facet is convex rather than flat as in *Giraffa* and is inclined laterally at a less steep angle. The process on the dorsal edge of the sivathere fibula is both less tall and less massive than that of *Giraffa*. The posterior tibial facet of the *Giraffa* fibula extends farther forwards towards the lateral edge. The calcaneal facet on the ventral surface of the fibula is both more elongate anteroposteriorly and more concave in *Sivatherium*.

Calcaneum

Sivathere and giraffine calcanea are difficult to separate. Even with the aid of associated skeletal material of known genus, only one minor morphological feature serves to distinguish the two. Both *Sivatherium* and *Giraffa* calcanea have an elongate anteroventral facet on the inferior surface for articulation with the naviculocuboid. In *Giraffa* the posteromedial edge of the naviculocuboid facet extends dorsally on to the medial side of the anterior process of the calcaneum. The additional facet is apparently absent from *Sivatherium* calcanea.

Astragalus

Sivathere and giraffine astragali are very similar in morphology. Sivathere astragali tend to be larger in fully adult specimens. The only morphological feature serving to differentiate the two genera is that *Sivatherium* lacks the lateral notch that in *Giraffa* is present between the tibial trochlea and naviculocuboid trochlea. The validity of this distinguishing feature is questionable, for the lateral notch tends to be at least partly infilled in mature male specimens of *G. camelopardalis*.

Naviculocuboid

The *Sivatherium* naviculocuboid tends to be larger than that of *Giraffa*. On the dorsal (proximal) surface the articular facet for the calcaneum often extends farther posteriorly in *Giraffa*. The two articular facets for the astragalus are more markedly separated at their posterior edge in *Sivatherium* and the posterior edge of the lateral astragalus facet is not raised dorsally as in *Giraffa*. On the ventral (distal) surface the metatarsal facet is proportionately larger than that of *Giraffa* but giraffine naviculocuboids possess an additional transversely orientated facet for articulation with the posterior edge of the metatarsal and which is absent in *Sivatherium*.

Metatarsal

The *Sivatherium* metatarsal is shorter, wider and more massive than that of *Giraffa*. The proximal epiphyses differ slightly to reflect the different morphology of the distal naviculocuboid and, in addition, are larger in *Sivatherium*.

Remarks

Certain trends are evident in the evolution of African sivatheriid ossicones. These include reduction (and perhaps posterior migration) of the anterior ossicones, elongation and increase in torsion of the posterior ossicones, development of secondary bone apposition on the anterior edges of the posterior ossicones and increase in size of the basal sinus concomitant with increase in overall size.

The common morph of the posterior ossicones of *S. maurusium* (Type A of Harris 1974) could clearly have evolved from the condition seen in *S. hendeyi*. So far different morphs of *S. maurusium* ossicones (Types B and C of Harris 1974) have been recorded only from Bed II at Olduvai, but each morph is represented by several individuals. It is possible that the different ossicone shapes seen at Olduvai are indicative only that the ossicones of *S. maurusium* were variable and they thus have no taxonomic significance. It is, however, also possible that the African sivatheriids were as diverse as those from Asia and, as in some bovid tribes, specific differences are more immediately evident from the cornual protuberances than from other parts of the body. This question can be resolved only after the collection of further and more complete cranial material from different localities.

Another apparent evolutionary trend is seen in the metacarpals, those of *S. hendeyi* being longer than those of *S. maurusium* and *S. giganteum*. Metacarpals of *S. maurusium* appear to decrease in length through time. Shortening of the metatarsals is less marked and no pronounced trends have been observed in other elements of the skeleton or in the teeth.

TABLE 1

Measurements of *Sivatherium hendeyi* ossicones

	L12730 (posterior)	L31285 (anterior)
Length	450+	195+
Basal diameter ap . .	120	94
Basal diameter dv . .	92	
Basal diameter tr . .		71

TABLE 2

Measurements of *Sivatherium hendeyi* deciduous teeth

	L2047	L2048	L2049	L2358	L13051	L30475	L2540	L10179	L10809	L13315
DP^2 ap			35,9′							
tr			28,7′							
DP^3 ap		36,7			33,9					
tr		31,2			31,6					
DP^4 ap	38,5*			37,5	—					
tr	39,3			39,3	40,0					
DP$_3$ ap									35,8	32,6
tr									19,7	20,4
DP$_4$ ap							44,1	51,5		
tr							24,8	29,0		

TABLE 3

Measurements of *Sivatherium hendeyi* upper teeth

	L1865	L1873	L2046	L11352A	L12083
P^3 ap . . .		32,9			
tr . . .		44,5			
P^4 ap . . .	34,2				
tr . . .	41,5				
M^1 ap . . .			47,6*		
tr . . .			51,6		
M^2 ap . . .					53,2
tr . . .					54,2
M^3 ap . . .				51,9	
tr . . .				49,4	

TABLE 4

Measurements of *Sivatherium hendeyi* lower teeth

	L1839	L1876	L3468	L5468	L7247	L7248	L7249	L9161	L9163	L30875	L31137
P$_2$ ap											27,5
tr											17,4
P$_3$ ap						37,9		38,9			39,7
tr						28,5		27,1			26,3
P$_4$ ap				43,5	40,7		40,6	42,5			44,5
tr				31,5	28,2		28,5	29,3			31,9
M$_1$ ap		45,5	44,3					46,1		47,2	44,4
tr		32,4	34,4					30,6		35,0	33,8
M$_2$ ap								50,6	52,2		
tr								36,7	36,7		
M$_3$ ap	74,5′							71,5			64,2
tr	38,1′							34,7			33,1

TABLE 5

Measurements of *Sivatherium hendeyi* postcranial elements

SCAPULA	L20141	L3093	L22281	L20949	L1272	L12742					
Max length blade	600+										
Max width articular edge	141	164	177	162+	162	149					
Max width glenoid	91	97	127	120+	127	113					
Max depth glenoid	85		118		102	102					
HUMERUS	L3096	L2239	L3097	L3434	L8897	L12377	L6883	L21569			
Width lat epicondyle	187		149	187	167			133			
Width distal epiphysis	169				153		161	121			
Depth distal epiphysis	106				96*	116	102				
ULNA	L2242	L2243	L3112	L6036	L8069						
Depth olecranon ap (at junction of epiphysis)	115+	97	94+	100							
Width humerus facet tr	78	85			86						
Depth humerus facet ap	63	62	58	60	73						
RADIUS	L21569	L2240	L2241	L22139	L9813	L12844	L14355	L14177			
Length	625										
Proximal epiphysis tr	164	165		160							
ap	82	89		80				86			
Distal epiphysis tr	137		143			114	129				
ap	87		82		72	74	82				
METACARPAL	L4746	L20195	L3114	L14173	L19844	L12088	L9842	L7261	L4958	L7263	L20796
Length	350	400	415	390							
Proximal epiphysis ap	68	80	88	81	74		71			71	79
tr	100	108		121	109		108			74	113
Distal epiphysis ap	58	66	74	70		70		62	60		
tr	100	111	123	119		117		115	110		
	L6219	L5704	L12052B	L12742	L9843	L20860	L11864	L20240	L14174	L2245	L3111
Proximal epiphysis ap				78	72	71	80				
tr				108	106	115	113				
Distal epiphysis ap	68	63					65+	61	62	60	59+
tr	110	107					114	109	110	110	110+

TABLE 5 (*continued*)

TIBIA	L22186	L5420	L13972	L14244									
Length	580	530											
Proximal epiphysis ap													
tr	163	169											
Distal epiphysis ap	88	81	73	83									
tr	127	122	102	125									
FIBULA	L6096	L6097											
Max length ap	62	63											
Max breadth tr	36	36											
Max height dv	51	46											
CALCANEUM	L5399	L5896	L6334	L3106	L13970	L12658							
Length	210	219	208	200	225								
Width articular region	86	90	87		101								
Depth articular region	95	102	92	93	100	101							
Width tuber calcis	64	67	62		62								
Depth tuber calcis	72	74	63		66								
ASTRAGALUS	L7391	L7385	L7390	L25032	L12393	L7378	L7384	L12657	L3259	L7392	L7376	L4222	
Lat length	128				119	111	129	127	129	129		125	
Med length	114	106	102				109	104	117	109	109	106	
Width tibial trochlea	92						88	82	85+	83	84	77	
Width navcbd trochlea	84	75		73				82	90	84	81	81	
Depth ap	68	69	65	66	58			70′	82				
	L7393	L7381	L7382	L7387	L7377	L7378	L9827	L3550	L20853	L6207	L12745	L6028	L3094
Lat length	126				123	126		127	123	125		132	126
Med length	112	106	108	113	109	109	109	103	108	109	101	112	102
Tibial tr	93	80	76	98	86	85		87	93	94	87	92	85
Navcbd tr	86				76	83	79	81	83	87	83	84	80
Depth ap	74	64	70	78	69			68	75	74	72	76	
	L21820	L9830	L1242	L9829	L3092	L2238	L20851	L2233	L1263	L20242	L4233	L6027	L11753
Lat length		121	94	117	126	118	125	128	132	129	130	123	123
Med length	99	110	84	101	106	101	106	106	110	111	113	103	106
Tibial tr	91	90	67	86	77	87	87	81	88	87	95	88	93
Navcbd tr	79	82	64		81	87	79	79	80	87	79	75	81
Depth ap	69	69	55	69		73	72	70	76	75	71	74	72

Table 5 (*continued*)

NAVICULOCUBOID	L3109	L1800	L7632	L13679	L7896	L6029	L7406	L4229	L7359	L3798	L9219	L5157
Median length ap	99	104	113			108		112	108	107	94	99
Max width	102	108	114		100	112	97	106	95	106	103	98
Lateral depth dv	57	57	58	56	57	60	57	58	56	55	54	54

NAVICULOCUBOID	L14712	L4230	L7538	L11906	L12614	L14123	L3104	L9835	L2232	L13156	L4231	L4739
Med length	121			96			106	100	95	115	114	87
Max width	118	106	105	89	84	110	106	104	101	105	113	97
Lat height	58	59	57	54	50	65	57	52	57		57	51

METATARSAL	L5401	L20623	L7258	L13971	L12246	L1244	L7259	L12247	L21534	L7262	L9274	L14339	L14145
Length	410												
Proximal ap	89	100	98	66	66	68	68	99				93	85
tr	94	101	99	82		74	101						
Distal ap	58				63			70	63+	63	56		
tr	95				104			111	107	105	95		

Family **Giraffidae** Gray, 1821

According to Hamilton (1973) this family contains only paleotragines and giraffines. *Zarafa* from the early Miocene of north Africa is the earliest representative of the family and was assigned to the Paleotraginae although not on the direct lineage to later giraffines or paleotragines (Hamilton 1973, fig. 13). Giraffines appear to have been of Asian origin but the presence of *Giraffa* in the early Pliocene of South Africa may require some modification of the evolutionary sequence of *Honnanotherium*, *Bohlinia*, *Giraffa*, suggested by Bohlin (1935) and accepted by Hamilton (1973).

Subfamily Giraffinae Zittel, 1893

Three extinct giraffine species have been recognized in the late Pliocene and early Pleistocene localities of east Africa (Harris 1976). The smallest species, *Giraffa pygmaeus*, is known from ossicones and dentitions but postcranial remains have so far proved rare. The other two species, *G. gracilis* and *G. jumae*, are more completely represented in the fossil record although no complete crania have yet been found of *Giraffa gracilis*. The two larger extinct *Giraffa* species may be readily identified on the basis of ossicone morphology and orientation. The teeth and postcranial elements of all giraffine species are, however, very similar in morphology. Both the teeth and postcranial elements of *G. jumae* tend to be larger than those of *G. gracilis*, but owing to size variation and sexual dimorphism neither the teeth nor the skeletal elements of these two species can always be separated with certainty. The same is true of the teeth of *G. pygmaeus* and *G. gracilis* from Pliocene localities. It is unfortunate that so few associated giraffine cranial and postcranial remains have been retrieved to date but, taking into account the fragmentary nature of the Plio-Pleistocene giraffine remains from east Africa, the taxonomic criteria adopted by Harris (1976) appear to be valid.

Giraffa cf. *G. jumae* Leakey, 1965

Figs 4–9

Diagnosis

A diagnosis revising that of Leakey (1965) is given in Harris (1976).

Cranial remains

Ossicones

Only three giraffine ossicones have been retrieved from Langebaanweg. The best preserved specimens comprise a left and right ossicone from a single individual (SAM–PQ–L20940) collected from the Quartzose Sand Member. The individual was immature and neither ossicone had been fused to the cranium. The two ossicones are similar in morphology to, but rather smaller than, those of immature extant male giraffes. The lateral edge of each ossicone base is flat but the medial edge is expanded towards its fellow. Each ossicone tapers gradually above its base but a distinct terminal knob is present at the distal extremity. The posterior surface of the ossicone is slightly concave but the anterior surface is virtually flat, both as in *G. jumae*. The surface of each ossicone is cut by a number of irregular longitudinal grooves that are most pronounced on the anterior and median surfaces. As might be expected in an immature individual, there is little evidence of secondary bone apposition.

The third ossicone (SAM–PQ–L30960) is somewhat larger but is incomplete distally. The rugose nature of the bone within the basal cavity suggests that this specimen, too, was derived from an immature individual.

Dentition

A few nearly complete lower tooth rows are known but the majority of Langebaanweg giraffine teeth were isolated specimens. The teeth are, in general, a little larger than those of the extant *Giraffa camelopardalis* and than Eurasian fossil giraffine species (*G. priscilla*, *G. attica*, *G. punjabensis*, *G. sivalensis*). Though larger than the teeth from the type specimen of *G. jumae* from Rawe (Leakey 1965) they are of similar size to teeth of Late Pliocene and early Pleistocene specimens of *G. jumae* from other east African localities (Harris 1976, and in preparation).

Postcranial remains

The Langebaanweg giraffine postcranial elements have typical giraffine morphology. They are of similar size and proportions to those of extant male giraffes, larger than specimens of *G. jumae* from the Omo Basin (Coppens *et al.*, in preparation) but of similar size to the largest *G. jumae* specimens from the Ethiopian locality of Hadar (Taieb *et al.* 1974; Harris, in preparation). Differences in postcranial anatomy between the Langebaanweg giraffine and *Sivatherium hendeyi* have been discussed previously in this paper.

Remarks

In the absence of mature ossicones, whose orientation on the cranium can be determined, it is difficult to make a positive identification of the Langebaanweg giraffine. The known specimens are too large for *Giraffa pygmaeus* and the presence of a distinct terminal knob suggests that they do not belong to *G. gracilis*. They are slightly smaller than, but otherwise quite similar to, immature ossicones of *Giraffa camelopardalis* but could equally well belong to *G. jumae* (immature specimens of which are yet unknown) or even a new species. None of the three east African fossil giraffine species is clearly ancestral to *Giraffa camelopardalis* and the possibility that the extant giraffe was of South African origin, and perhaps descended from the Langebaanweg form, cannot be entirely ruled out. The acquisition of mature giraffine ossicones from Langebaanweg may in future solve the problem. Meanwhile, because the teeth are rather larger than those of extant giraffes and, on balance, the postcranial elements are rather more robust than the latter, the Langebaanweg giraffine is provisionally assigned to *Giraffa* cf. *G. jumae*.

TABLE 6

Measurements of *Giraffa* cf. *G. jumae* ossicones

	L20940 (l)	L20940 (r)	L30690
Length	177	177	
Basal diameter ap	86	92	112
Basal diameter tr	59	59	

TABLE 7

Measurements of *Giraffa* cf. *G. jumae* deciduous teeth

	L6606	L13510	L13043 (l)	L13043 (r)	L10938	L10939	L10800
DP^2 ap			23,3	23,3	24,3		
tr			19,4	19,7	17,4		
DP^3 ap	26,1		27,1	26,8		27,7	28,8
tr	21,8	20,3	22,6	23,7		24,4	26,5
DP^4 ap			27,5	28,2			
tr			27,4	28,3			

	L30057	L2543	L6022	L11617	L2541
DP_2 ap	19,6				
tr	10,9				
DP_3 ap	25,8				
tr	14,4				
DP_4 ap	36,2	38,2	32′		33,9*
tr	19,1	18,6	17′	16,5′	18,6′

TABLE 8

Measurements of *Giraffa* cf. *G. jumae* upper teeth

	L30126	L22021	L31138	L10343 (l)	L10343 (r)
P^2 ap		22,3			
tr		26,5			
P^3 ap	25,0				
tr	27,4				
P^4 ap	25,6				
tr	28,2				
M^1 ap				31,3	29,2
tr				33,1	33,7
M^2 ap			33,0	33,4	31,6
tr			37,1*	34,8	36,1
M^3 ap			35,2		
tr			36,8		

TABLE 9

Measurements of *Giraffa* cf. *G. jumae* lower teeth

	L22021	L5767	L31138	L20987	L4773
P_2 ap			23,0		
tr			14,4		
P_3 ap			27,0	23,6	
tr			20,1	19,7	
P_4 ap			28,5	24,4	26,1*
tr			22,7	22,1	20,6
M^1 ap	27,5		33,1	27,5	
tr	22,2	23,5	23,7	24,4	
M_2 ap		31,3	32,9	30,0	
tr		25,3	25,3	24,6	
M_3 ap			46,9		
tr			25,0		

TABLE 10

Measurements of postcranial elements of *Giraffa* cf. *G. jumae*

HUMERUS	L9933	L3095	L12372	L20951	L14148	L6950	L6355	L6884	L6949
Width lat epicondyle	117	126		127	124	123			138
Width distal epiphysis	115	121		138	119	128			134
Depth distal epiphysis	110	113	85+	99	96	90	81+	77+	103

ULNA	L6037	L13500
Depth olecranon process at epiphysis junction . .	93	94
Width humerus facet tr	65	59
Depth humerus facet ap	65	60

RADIUS	L4962	L7922	L7994	L5233	L13500
Proximal epiphysis tr	134		118		129
ap	75		68		69
Distal epiphysis ap .		108		119	
tr .		79		89	

METACARPAL	L22282	L20859	L11509	L13687	L6035	L5488	L12734A	L7268	L5303	L7267	L9282	L7264
Proximal epiphysis ap	66		70	66	70	64	68	63	64			
tr	99		98+	103	98	96+	105	95	97			
Distal epiphysis ap .		65								58+	66	60
tr .		96								99		88

TIBIA	L1797	L13528	L14308	L11527	L6030	L20863	L20866	L14352
Length	655	590						
Prox ap . . .							121	
tr		156						
Dist ap . . .	89	76	86	92	80	64		82
tr	114	113	114	120+	111	94		114

FIBULA	L13001	L12231
Max length ap . .	71	70
Max breadth tr . .	36	34
Max height dv . .	53	46

Table 10 (*continued*)

CALCANEUM	L4875	L14193	L11568	L4879	L7369	L20268	L2230	L21818	L5897	L4228	L20629	
Max length	213	238	233	209	196	224	228	205			192	
Max articular width	99	106	85	80	86	96	85	87	77	66		
Max articular depth	105	108	93	93	92	114	107	97	99	84	91	
Width tuber cacis	67	77	68	52	50	67	64	55			53	
Depth tuber calcis	63	81	80	63	58	75	71	57				
ASTRAGALUS	L4919	L20852	L7386	L1241	L2082	L9826	L20950	L1241	L12184	L21913	L24920	
Lat length	107	123	107	111	119	115	116	107	111	118	126	
Med length	97	104	97	98	110	104	102	94	100	108	106	
Tibial trochlea tr	72	82	70	72	72		78	76	75	81	89	
Navcbd trochlea tr	64	74	69	67	70	69	74	68	75	74	80	
Max depth	58	67	64	58	67		64	63	61	68	71	
	L14190	L5400	L11754	L9218	L7388	L12384	L4224	L7383	L22180			
Lat length	122	115	125	105	115	116	118	109	128			
Med length	107	97	107	92	101	99	104	98	110			
Tibial tr	84	85	85	71	73	74	79	69	79			
Navcbd tr	79	78	75	65	73	70	74	64	79			
Max depth	71	72	74	59	61	63	67	60	76			
NAVICULOCUBOID	L5158	L5159	L1264	L6100	L11571	L3897	L7360	L7353	L7356	L7357	L7365	L7354
Med length ap	103	101	89	97	98			108		106	93	
Max width tr	97	96	91	87	95	86	89	103	93	91	87	87
Lat height dv	45	51	50	47	46	48	48	50	47	54	49	47
METATARSAL	L6227	L5304	L7282	L22158	L14188	L6069						
Prox ap	87		92		98							
tr	85		84		94							
Dist ap		60		59		64						
tr		86		88		87						

DISCUSSION

The giraffoids from Langebaanweg are almost certainly the earliest representatives of their respective genera yet reported from Africa although confirmation of their age must await detailed investigation of other elements of the fauna. If an early Pliocene age is substantiated the two Langebaanweg giraffoids are of similar if not earlier age than their nearest Asian relatives and the question of Asian versus African origin of the giraffines and later sivatheriids will need to be reinvestigated.

Hamilton (1973) assigned *Prolibytherium* to the Sivatheriidae and suggested that sivatheriids and giraffids were independently derived from Oligocene Dremotheriidae. *Prolibytherium* shares many morphological features with dremotheriids and primitive cervids and may, perhaps, be better assigned to one of these families. The evidence for sivatheriid affinity is not conclusive and, as Hamilton himself points out (1973, fig. 13), if placed in the Sivatheriidae *Prolibytherium* can be only distantly related to other known members of the family.

As is evident from *Sivatherium hendeyi*, a foreshortened anterior limb is not a primitive feature of *Sivatherium* but a character acquired during the evolution of this genus. Moreover, the posterior ossicones of *S. hendeyi* are relatively short, narrow and unornamented, suggesting that the palmate posterior ossicones of *S. giganteum* and the more complex examples of *S. maurusium* are advanced features. The disposition of the ossicones of *S. hendeyi* is not dissimilar to that of *Giraffokeryx* (Colbert 1933). It is not implausible that *Sivatherium* and related genera were relatively late (upper Miocene?) offshoots from paleotragine stock. If so, relegation of the family Sivatheriidae to a subfamily of the Giraffidae might appear warranted.

Abundant giraffine material is known from Hadar in Ethiopia (Harris, in preparation) and Laetolil in Tanzania (Harris, in preparation). The earlier horizons from Hadar are dated in excess of 3 m.y. (D. C. Johanson, pers. comm.) and the Laetolil faunas are believed to be between 3,25 and 3,75 m.y. (M. D. Leakey, pers. comm.). Occurring at both localities are representatives of the three species known from east African Pleistocene localities. Giraffines have not yet been reported from Lothagam and Kanapoi but a few undescribed and incomplete specimens are known from Lukeino which have been dated at between 5,4 and 6,7 m.y. (Pickford 1975). The subfamily Paleotraginae is currently being revised (W. R. Hamilton, pers. comm.) and perhaps in the near future further east African material will be available to help place the Langebaanweg giraffines in their proper context.

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ABBREVIATIONS

ap	anteroposterior	Lat	lateral
dv	dorsoventral	prox	proximal
tr	transverse	dist	distal
	estimated measurement	med	medial
*	approximate measurement	navcbd	naviculocuboid
Max	maximum	tr	trochlea (astragalus measurements only)

6. SYSTEMATIC papers must conform with the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

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Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (*Lembulus*) *bicuspidata* (Gould, 1845)

Figs 14–15A

Nucula (*Leda*) *bicuspidata* Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (figs 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:
comma separates author's name and year
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In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33.51S, 25.39E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers, date and geographical positions.

7. SPECIAL HOUSE RULES

Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '. . . the Figure depicting *C. namacolus* . . .'; '. . . in *C. namacolus*(Fig. 10) . . .'

(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
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(c) Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

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Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

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